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20 FEBRUARY 1980

(FOUO 2/80)

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JPRS L/8934

20 February 1980

USSR Report

AGRICULTURE

(FOUO 2/80)



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VARIABILITY OF NATURE OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT AS RELATED TO VEGETATION CONDITIONS

Novosibirsk SIBIRSKIY VESTNIK SEL'SKOKHOZYAYSTVENNOY NAUKI in Russian No 2, 1974 pp 31-39

[Article by R. A. Tsil'ke, candidate of agricultural sciences, Siberian Scientific Research Institute of Agriculture]

[Text] Most economically useful characters are referable to the quantitative category, and each of them is controlled by many genes. In the course of ontogenesis, each character is formed as a result of complex interaction between the genotype and the environment. Allele and nonallele interaction of genes and interaction between the genotype and numerous environmental factors create enormous possibilities for phenotypic variability. Quite a few difficulties arise in singling out the effects of individual genes or blocks of genes on development of a character. In breeding work, one constantly observes high variability of manifestation of a character when even the same genotype is raised under different vegetation conditions. When working with hybrid material, additional difficulties arise at the early stages of the breeding process, when selecting and evaluating strains, which is related to variability of the nature of inheritance of a character and interaction of the genotype with the environment. Breeders make some serious mistakes when they begin selection according to quantitative characters, particularly grain yield, in segregating generations (F_2 , F_3) without determining the nature of inheritance thereof under specific conditions. Suffice it to indicate that selection will not be effective if the increase in manifestation of a character in a selected line, as compared to the parental pair, is due to the heterosis effect attributable to heterozygosity. This effect is not fixed by selection. Unfortunately, selection is often made without consideration of these truths and, of course, it fails.

Studies conducted more recently in different countries indicate that there are many questions in the problem of inheritance that are still unanswered. In view of the variability of nature of inheritance and distinctions of the Siberian climate, it is imperative to conduct broader research in the next few years on genetics of qualitative and quantitative characters in different ecological zones of that region.

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We discuss here experimental data on variability of degree and nature of inheritance and heritability of quantitative characters on the example of one hybrid combination. The simple model of analysis of inheritance of economically useful characters can be used in breeding practice.

Material, Methods and Conditions of Investigation

We took zoned cultivars Saratovskaya 29 and Mil'turum 553 for the crosses; each of these cultivars is characterized by a set of economically valuable characters. Both cultivars are highly productive, and the productivity components consist of different biological properties and cultivars. Mil'turum 553 is notable for exceptional adaptation to the steppe and forest-steppe conditions of Siberia, high degree of ecological resistance to drought due to retarded rate of development during the period between tillering and heading. Saratovskaya 29 is highly productive, the grain is notable for high baking and technological qualities. The adverse characters of both cultivars include low resistance to leaf rust and lodging, and this applies in particular to Saratovskaya 29 wheat. However, modern breeding programs make it possible to correct these flaws within a relatively short period of time by means of proper organization of back crossing with the use of a provocative background and accelerated reproduction of breeding material (2-3 generations per year). In view of the many valuable properties of the above cultivars, they and their derivatives must continue to be used as base material for breeding, at least until cultivars are developed for nonirrigated cultivation.

The crosses were performed in 1969. The first generation for producing F_2 seeds was raised in the hothouse in the winter of 1970-1971. The field experiment was started in 1971 and 1972. The precursor was a fallow field in 1971 and rotation of a cover of perennial grasses in 1972. Sowing was done on 25 May. The seeds were sown with a manual sower in rows 200 cm long with a nutrition area of 10x30 cm. We planted 10 rows for each base cultivar and F_1 hybrid, and 20 rows for the F_2 hybrid. The experiments were repeated twice. The agrotechnology applied was the usual one for the local conditions. During the period between tillering and heading, the plants were dusted with vofatoks [metaphos--methyl parathion] every 2-3 days to control "skrytostebel'nyye" [stem-boring?] pests. A record was kept of heading phase for each plant. In 1972, the field yield was lower on the average for all variants than in 1971, and this is related chiefly to destruction of shoots by wireworms (Table 1). At the start of the full-ripe stage (1971) and end of the yellow-ripe stage (1972) the plants were pulled out, dried and analyzed for structural elements. We grouped the experimental data and calculated the main statistical indices according to Rokitskiy [6].

Vegetation conditions differed appreciably in different years. In 1971, there was 16 mm more precipitation in June than the many-year norm and 54 mm less in July. Mean daily air temperature was the same in June, it was 2°C higher in July and 1.5°C lower in August than perennial average. The relatively high temperatures and minimal precipitation in July created

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unfavorable conditions for wheat development at the heading and flowering stages. In 1972, there was 29 mm more precipitation in June than the mean perennial norm, 21 mm more in August and 16 mm less in July. Air temperature was 1.1°C lower in June, 1.4°C lower in July and 1.1°C lower in August than the perennial mean. The significant shortage of warmth with good amount of precipitation caused slower development of plants at all stages, starting with heading. The conditions were extremely unfavorable during the period of grain maturation. In spite of the late harvesting, it never did reach full ripeness, and in late August it was exposed to low temperatures, which led to winterkill of the grain.

Table 1. Data on germination and survival of plants

Cultivars and hybrids	1971					1972				
	seeds planted	germinated plants	%	plants retained heading time	plants remaining	seeds planted	germinated plants	%	plants retained heading time	plants remaining
P1--Saratovskaya 29	400	337	84	309	92	400	318	80	262	82
P2--Mil'turum 553	400	382	95	312	82	400	323	81	293	91
F1--Saratovskaya 29	400	381	95	323	85	400	298	75	237	80
F2--Saratovskaya 29	400	381	95	323	85	400	298	75	237	80
Mil'turum 553	400	381	95	323	85	400	298	75	237	80
Mil'turum 553	800	717	90	584	81	800	595	74	508	85

Experimental Section and Discussion

Table 2 lists data on degree and nature of inheritance of quantitative characters. The germination to heading period is closely related to the duration of the vegetation period and, although this character is genetically determined, environmental conditions have an appreciable effect on degree thereof. The initial cultivars differed substantially with regard to duration of this period: the difference constituted 7 days in 1971 and 10 days in 1972. In 1972, the sprouting-heading period was longer than in 1971: 9 days longer for Saratovskaya 29, 12 days longer for Mil'turum 553, F₁ and F₂ hybrids. In 1971, the first hybrid generation was similar to the average ripe Saratovskaya 29 parent, i.e., there was manifestation of partial dominance. In 1972, F₁ differed from the mean between parents by only 1 day, in the direction of the cultivar with a shorter period (Saratovskaya 29), with expression of intermediate inheritance and partial dominance. The period was 2 days longer at the F₂ stage than F₁.

Overall (number of stems) and productive (number of productive stems--heads) tillering depends significantly on plant nutrition area and environmental conditions. In 1971, the differences between cultivars were statistically unreliable, whereas in 1972 the varieties differed appreciably both with respect to overall and productive tillering. In 1972, there were more

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tillers per plant than in 1971: 2.7 more for Saratovskaya 29, 6.9 more for Mil'turum 553, 3.6 more for F_1 and 4.0 more for F_2 . There was expression of overdominance in F_1 in 1971 and partial dominance in 1972. In the second generation there was a negligible decrease in number of stems, as compared to F_1 . Analogous results were obtained for productive tillering.

The initial cultivars differed substantially in stem length: the difference was 6 cm in 1971 and 15 cm in 1972. In 1971, Saratovskaya 29 had the longer stem and in 1972 it was Mil'turum 553. In 1972 the stem was longer than in 1971: by 29 cm for Saratovskaya 29, 50 cm for Mil'turum 553, 28 cm for F_1 and F_2 . Consequently, this character was more stable in the hybrid than the cultivars. There was expression of overdominance in the first hybrid generation in 1971 and intermediate inheritance in 1972. As compared to F_1 , stem length diminished in the second generation.

The top internode is a component of overall stem length; however, these characters differ in nature of inheritance and reaction to environmental conditions. In 1971, the cultivars differed appreciably in internode length, while in 1972 the differences were unreliable: in the former case, the difference constituted 8 cm and in the second 1 cm. In 1972, the internode was longer than in 1971: by 14 cm for Saratovskaya 29, by 21 cm for Mil'turum 553, by 13 cm for F_1 and by 12 cm for F_2 . In 1971, there was expression of overdominance in F_1 , and in 1972 there was complete dominance in the direction of the parent with the longer internode. There was a reliable reduction in internode length in the second generation, as compared to F_1 , in both 1971 and 1972.

The cultivars also differed in spike [head] length: the difference constituted 20 mm in 1971 and 23 mm in 1972. The spike was longer in 1972 than in 1971: by 7 mm for Saratovskaya 29, 10 mm for Mil'turum 553, 5 mm for F_1 and F_2 . There was greater fluctuation in different years for the cultivars than the hybrids. In 1971, there was expression of partial dominance in F_1 and in 1972 intermediate inheritance with partial dominance in the direction of the parent with the longer spike (Mil'turum 553). The spike was reliably shorter in the second generation than in the first.

The plants differed in number of spikelets per spike: the difference constituted 4.5 in 1971 and 4.1 in 1972. In 1972, more spikelets were formed per spike than in 1971: 2.0 more for Saratovskaya 29, 1.6 more for Mil'turum 553, 1.5 more for F_1 and 1.3 more for F_2 . There was wider fluctuation in the cultivars than the F_1 and F_2 hybrids. In the first generation, there was expression of intermediate inheritance with partial dominance in the direction of the parent with the larger number of spikelets per head. In the second generation, there was a negligible decrease in number of spikelets, as compared to F_1 , but it was statistically reliable.

The original cultivars differed reliably in weight per 1000 kernels, and the differences were particularly great in 1972. In 1971, the difference constituted only 2.4 g, and in 1972 it was 7.5 g. In 1972, the weight per

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1000 kernels was higher than in 1971: by 6.5 g for Saratovskaya 29, by 1.4 g for Mil'turum 553 and by 1 g for F_1 and F_2 . In the hybrid, this character was more stable than in cultivars, especially large-kernel Saratovskaya 29. In 1971, there was manifestation of overdominance in F_1 and in 1972 there was intermediate inheritance. The weight per 1000 kernels dropped in the second generation, as compared to the first.

The varieties did not differ reliably in 1971 with regard to number of kernels per head, whereas in 1972 the difference constituted 9 kernels. More kernels were formed per head in 1972 than in 1971: 9 more for Saratovskaya 29, 1 more for Mil'turum 553, 4 more for F_1 and 3 more for F_2 . In 1971, there was manifestation of overdominance in F_1 , whereas in 1972 there was complete dominance in the direction of the parent with the larger number of kernels per head (Saratovskaya 29). The second generation did not differ reliably from the first according to this character.

There is a close relationship between kernel weight per head, number of kernels per spike and weight per 1000 kernels. The base cultivars differed substantially according to this character: the difference constituted 0.10 g in 1971 and 0.54 g in 1972. The kernels weighed more in 1972 than in 1971: 0.52 g more for Saratovskaya 29, 0.08 g more for Mil'turum 553, 0.09 g more for F_1 and 0.05 g more for F_2 . In 1972, there was manifestation of overdominance in F_1 , whereas in 1972 there was intermediate inheritance with partial dominance in the direction of the best parent. In the second generation, grain weight per spike diminished reliably, as compared to the first generation, mainly as a result of reduction in kernel size (weight per 1000 kernels).

The number of kernels per plant is closely related to the number of kernels per head and number of productive spikes. In 1971, the initial cultivars did not differ reliably; the difference was reliable in 1972 and constituted 73 kernels. On the average, more kernels were formed per plant in 1972 than in 1971: 165 more for Saratovskaya 29, 233 more for Mil'turum 553, 176 more for F_1 and 148 more for F_2 . In both 1971 and 1972, there was manifestation of overdominance in the first generation. In the second generation there was a decrease in number of kernels, as compared to F_1 ; however, the differences are statistically reliable.

The initial cultivars did not differ reliably in the years of our studies with regard to grain weight per plant. The grain weight was higher in 1972 than in 1971: by 7.6 g for Saratovskaya 29, by 7.4 g for Mil'turum 553, by 5.6 g for F_1 and by 4.4 g for F_2 . There were fewer fluctuations in the 2 years among F_1 and F_2 hybrids. Overdominance was manifested in the first generation, and kernel weight decreased reliably in the second generation.

The obtained results indicate with a high degree of reliability that not only the degree of quantitative characters but nature of inheritance by hybrids change under environmental influences. The different reactions of initial parental and hybrid genotypes to changing environmental conditions lead to a change in inheritance, since the latter is demonstrable by comparing the intensity of the character in the F_1 hybrid and original parents.

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Table 2. Degree of expression of quantitative characters in original parents, F₁ and F₂ hybrids
($\bar{x} \pm s_{\bar{x}}$)

Characters	1971			1972		
	Sara- toysk. 29	Mil'- turum 553	\bar{x}	in- heri- tance	\bar{x}	in- heri- tance
Germination-heading period, days	40±0.1	47±0.1	41±0.1	PD	53±0.2	55±0.2 IPD
Tillers/plant	5.5±0.14	5.8±0.16	7.7±0.12	OD	11.3±0.28	11.4±0.28 PD
Heads/plant	5.4±0.13	5.6±0.16	7.6±0.15	OD	10.9±0.28	10.4±0.21 PD
Stem height, cm	72±0.5	66±0.7	80±0.6	OD	107±0.7	102±0.9 I
Length of top internode, cm	40±0.4	32±0.4	42±0.5	OD	55±0.4	51±0.5 CD
Length of head, mm	92±0.6	112±0.9	109±0.8	PD	114±0.8	110±0.6 IPD
Spikelets/spike	13.5±0.1	18.3±0.1	17.0±0.1	IPD	18.5±0.1	18.1±0.1 IPD
Wt./1000 kernels, g	31.6±0.25	29.2±0.27	35.1±0.26	OD	34.1±0.30	31.2±0.31 I
Kernels/head	36±0.6	35±0.6	40±0.6	OD	46±0.5	43±0.6 CD
Wt. kernels/head, g	1.11±0.02	1.37±0.02	1.28±0.02	OD	1.46±0.03	1.33±0.03 IPD
Kernels/plant	191±5.7	196±6.2	304±7.4	OD	339±9.7	445±10.7 OD
Wt. kernels/plant, g	6.0±0.2	5.7±0.2	10.7±0.3	OD	13.1±0.4	13.9±0.4 OD

Key: I) intermediate inheritance

CD) complete dominance

PD) partial dominance

IPD) intermediate inheritance with partial dominance

OD) overdominance [or superdominance]

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In 1971, there was expression of overdominance for 9 characters in F_1 , partial dominance for 2 and intermediate inheritance with partial dominance for 1 character. In 1972, there was manifestation of overdominance for 2 characters, complete dominance for 2, intermediate inheritance with partial dominance for 3 and intermediate inheritance for 3 others.

The question arises: Can one assess gene action on the basis of phenotypic manifestation of a character? After all, such concepts as dominance, overdominance and intermediate inheritance are usually related by researchers to allele and nonallele gene interaction. As we know, the type of gene action is determined by the phenotypic expression. For this purpose, there are special methods of genetic analysis (in particular, diallele analysis) that permit determination, with varying degrees of precision, the action of genes in manifestation of the character in the phenotype. The simple model of genetic analysis that we used does not enable us to single out all types of action of genes that control quantitative characters. Moreover, manifestation of these characters changes markedly under the influence of environmental conditions. Apparently, there are no grounds to believe that superiority of F_1 over the best parental cultivar for some character is related solely to allelic interaction of genes (dominance, overdominance). Most probably, we are dealing here with nonallelic gene interaction also; however, it is not demonstrable. Hence, the applied concepts of dominance (incomplete, partial, complete) and overdominance reflect only the actual expression of a character in the phenotype under specific environmental conditions. The breeder, who has to derive conclusions about the nature of inheritance of economically useful characters on the basis of analysis of the first and second generations of each hybrid combination represented at the early stages of the breeding program, more often has to deal with expressly such a situation. It should be added that variability of the nature of inheritance as a function of vegetation conditions creates a number of difficulties in breeding, especially when solving problems of selection and evaluation of breeding material at the early stages.

In this regard, let us consider the data about the heterosis effect (Table 3). We know that the heterosis effect is defined either as superiority of the F_1 hybrid over the mean between parents or over the best parent. In the former case, heterosis is considered to be a phenomenon determined by dominance and in the latter by overdominance [7]. In reality, however, heterosis is the result of complex allelic and nonallelic interaction of genes and the genotype as a whole with the environment. In 1971, the F_1 hybrid was reliably superior to the mean among parents for 11 characters, including 8, for which it was superior to the best parent. In 1972, the F_1 hybrid exceeded the mean for the parents in 6 characters and the best parent in 2. The high heterosis effect according to number of kernels (55%) and weight of kernels per plant (76%) in 1971 is made up essentially of such elements as productive tillering (36%), weight per 1000 kernels (10%), number of kernels (11%) and kernel weight per head (23%). In 1972, the heterosis effect according to number of kernels (12%) and kernel weight (20%) per plant is attributable mainly to productive heading, number of

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kernels and kernel weight per head, i.e., characters that presented in F_1 incomplete, complete and partial dominance, respectively. Consequently, while the heterosis effect for kernel yield was induced primarily by manifestation of overdominance in 1971, in 1972 it was attributable to different degrees of dominance of characters that make up the productivity of the head and plant. In the example discussed, the relative rate of development of the cultivars and hybrids is of decisive significance to instability of inheritance, and this, in turn, caused substantial changes in expression of other quantitative characters. In 1971, the F_1 hybrid was similar to the Saratovskaya 29 cultivar according to rate of development. Under the conditions prevailing that year, there was fuller expression of the superiority of the heterozygote over the homozygotes. Actually, the heterozygote did not reach the level of the best parent with regard to only two traits, spikelets per head and head length. There was utterly different expression of genotypes of the cultivars and hybrid in 1972. With the cool and humid vegetation period then, the heterozygote did not manifest a statistically reliable effect of dominance of accelerated development, and it occupied an intermediate position between the parents. This predetermined the nature of inheritance of the rest of the traits in F_1 , in which there was manifestation primarily of the dominant and additive effect of genes.

Table 3. Manifestation of heterosis effect in the first hybrid generation, %

Characters	1971		1972	
	$\frac{\bar{x}_{F_1} + \bar{x}_{P_1}}{2}$	\bar{x}_{P_1} best parent	$\frac{\bar{x}_{F_1} + \bar{x}_{P_2}}{2}$	\bar{x}_{P_2} best parent
Tillers/plant	136	133	108	89
Heads/plant	138	136	110	92
Stem length	116	111	99	92
Length of top internode	117	105	104	103
Spike length	107	97	108	91
Spikelets/spike	106	99	104	93
Weight per 1000 kernels	116	111	99	89
Kernels/spike	113	111	106	96
Weight kernels/spike	129	123	116	90
Kernels/plant	158	155	122	112
Weight of kernels/plant	182	176	122	120

Table 4 lists the heritability indices calculated according to Purdy and Crane [8]. They differed substantially in the two years with regard to most characters, and this shows the need for studying hybrid combinations under different conditions before predicting the effectiveness of selection. Although the index of heritability does include the variability component, which is determined by heterozygosity and not fixed by selection, it still reflects the share of genotypic variability in overall phenotypic variability of the second generation. In 1971, the indices ranged from 0.13 to 0.53, depending on the trait, and from 0.17 to 0.70 in 1972. It should be noted that they are not high enough to expect great effectiveness from

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selection according to traits that are related to productivity of the spike. The relatively high indices for inheritance of stem and top internode length in 1972 are attributable to the fact that with the cool summer and fall there was expression of hybrid dwarfism in F_2 (deficiency), which increased variability of these characters.

Table 4. Indices of heritability

Characters	1971	1972
Duration of shoots-heading period	0.53	0.42
Number of stems per plant	0.43	0.28
Number of productive stems per plant	0.34	0.17
Stem length	0.26	0.70
Length of top internode	0.13	0.60
Length of head	0.34	0.30
Spikelets per head	0.48	0.35
Kernels per head	0.18	0.49
Kernel weight per head	0.30	0.51
Number of kernels per plant	0.42	0.30
Kernel weight per plant	0.34	0.25

Typically enough, the original cultivars did not differ in grain yield, either in 1971 or 1972; however, we observed substantial differences in each of the elements of harvest structure. Since they are genotypically determined, we could expect that homozygous recombinants, which would be superior to the initial cultivars in grain yield, would appear in the hybrid as a result of segregation. Such recombinants should contain the head length and number of spikelets inherent in Mil'turum 553, the head density, number of kernels per head and kernel size inherent in Saratovskaya 29. Our objective here did not include consideration of questions of correlation, selection and transgression of quantitative characters.

The obtained experimental data indicate that the nature of inheritance, indices of heritability and expression of quantitative characters depend on environmental conditions to a significant extent. This information is needed to develop effective breeding programs.

Conclusions

1. There was expression of overdominance in 9 out of the 12 quantitative characters of the F_1 hybrid (Saratovskaya 29 \times Mil'turum 553) that we studied in 1971, incomplete dominance of 2 traits, intermediate inheritance with partial dominance of 1; in 1972, there was superdominance of 2 traits, complete dominance of 2, intermediate inheritance with partial dominance of 3 and intermediate inheritance of 3 others.

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2. In 1971, the F_1 hybrid was superior to the mean among parents for 11 traits, superior to the best parent for 8 characters, the figures being 6 and 2, respectively, for 1972. The heterosis effect fluctuated in F_1 (in relation to best parent): 11 to 76% in 1971 and 12 to 20% in 1972.
3. The index of heritability (in the general sense) differed substantially in the 2 years. In 1971 it ranged from 0.13 (length of top internode) to 0.53 (duration of sprouting--heading period) and in 1972 from 0.17 (number of productive heads) to 0.70 (stem length).

BIBLIOGRAPHY

1. Borojevic, Slavko "Type of Inheritance and Heritability of Quantitative Traits in Hybrids of Different Wheat Cultivars," SAVREMENA POLJOPR. [Modern Agriculture (Croatian)], Vol 13, No 7-8, 1965, 587-606.
2. Chapman, S. R., and McNeal, F. H. "Gene Action for Yield Components and Plant Height in a Spring Wheat Cross," CROP SCI., Vol 11, No 3, 1971, 384-386.
3. Hsu, P., and Walton, P. D. "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54-60.
4. Jankovic, Milanka "Inheritance of Stem Length and Number of Kernels in Wheat," SAVREMENA POLJOPR., Vol 17, No 7-8, 1969, 781-786.
5. Sinitsyna, S. M. "Inheritance of Head Length in Soft Wheat," ZAPISKI LENINGRADSKOGO S.-Kh. IN-TA [Records of Leningrad Agricultural Institute], 124, No 1, 1968, pp 14-19.
6. Rokitskiy, P. F. "Biological Statistics," Minsk, Izd-vo Vysshaya Shkola, 1964, p 328.
7. Brubecker, J. L. "Agricultural Genetics," Moscow, Kolos, 1966, p 223.
8. Purdy, J. L., and Crane, P. L. "Inheritance of Drying Rate in 'Nature' Corn (Zea Mays L.)," CROP SCI., Vol 7, No 4, 1967, 294-297. [485-10,657]

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MONOSOMIC ANALYSIS OF KERNEL WEIGHT PER HEAD OF SOFT SPRING WHEAT

Novosibirsk IZVESTIYA SIBIRSKOGO OTDELENIYA AKADEMII NAUK SSSR SERIYA BIOLOGICHESKIKH NAUK in Russian Vol 15, 1974 pp 85-90

[Article by I. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 24 Dec 73]

[Text] F₁ and F₂ hybrids obtained by crossing 21 monosomic lines of Chinese Spring cultivar with Mil'turum 553, disomic F₁ and F₂ hybrids and the original cultivars were studied under field conditions in 1971-1972. In 1971, 13 monosomic F₂ hybrids differed reliably from the disomic F₂ hybrid with respect to weight of kernels per spike, and in only one case (1B) was the monosomic hybrid superior to the disomic one. In 1972, 15 monosomic F₁ hybrids and 11 F₂ hybrids differed reliably from the F₁ and F₂ disomic hybrid, and in 4 cases (2A, 1B, 5B, 6D) the weight of kernels per head was higher in the monosomic hybrid; in all other cases it was lower than in the disomic hybrid. We observed significant hybrid × year interaction. Maximum effectiveness in the monosomic state was manifested for chromosomes 2A, 5A, 7A, 1B, 3B, 4B, 1D, 2D, 3D, 4D, 5D, 6D and 7D. It is assumed that grain weight per head is controlled by many genes with complex allelic and nonallelic interaction, but the additive action is the chief element.

The techniques for cytogenetic analysis of qualitative and quantitative characters of wheats were described in detail in a number of works [1-4]. Methods of aneuploid analysis, as related to use thereof in genetic and breeding research on wheat, were discussed in the collective monograph entitled "Cytogenetics of Wheat and Its Hybrids" [5].

The wheat spike consists of a complicated set of characters with breeding and taxonomic importance. Different combinations and expressions of elements of head structure create a wide diversity of forms and density and, consequently, of productivity. Spike kernel weight is directly related to its size and number of kernels, while the latter is related to the number of

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spikelets and number of kernels per spikelet. Each element of the spike is controlled by many genes with different action and interaction. The expression of each spike element depends both on the genotype and environmental conditions.

Since quantitative characters are controlled essentially by genes with additive action, the monosomic state should rule out part of the genetic information needed for normal development of a trait. By comparing each of the 21 monosomic hybrids (or, more precisely, a mixed hybrid according to chromosomal constitution) to a disomic hybrid one can demonstrate, if not all of the chromosomes, at least those in which the genes with the main effects are located. Probably both the first and second generation hybrids can be used for this purpose. However, it should be noted that monosomic analysis cannot demonstrate all of the types of action and interaction of genes that control quantitative characters.

The working hypothesis that we adhered to in planning and conducting the experiment was discussed in [6]. The results of monosomic analysis of stem length and head density were reported previously [7, 8]. In this article, we submit the results of analysis of kernel weight per spike. This trait is referable to the category of quantitative characters, and there is no doubt that it is controlled by a large number of genes with different types of action. It can be assumed that genes having some influence or other on head productivity are localized in all chromosomes. Our objective was to demonstrate the effects of different chromosomes on one of the main traits, weight of kernels in a single head. To do this, we compared monosomic F_1 and F_2 hybrids to disomic F_1 and F_2 hybrids.

Material, Methods and Conditions

We used cytologically identified monosomic plants (σ^7) referable to 21 lines of Chinese Spring cultivar and crossed them with Mil'turum 553 (σ^7). The field experiment was set up on the experimental field of the Siberian Scientific Research Institute of Agriculture in 1971 and 1972 using the methods described in [8].

Variants of Experiment

1. Mil'turum 553 ($2n = 42$) (σ^7).
2. Chinese Spring ($2n = 42$), base cultivar of the monosomic lines.
3. The first generation hybrids (F_1) from 21 combinations of Mono-Chinese Spring \times Mil'turum 553. The hybrids are a population with the following genotypes: $2n-1 = 41$ ($\approx 75\%$) and $2n = 42$ ($\approx 25\%$).
4. Second generation hybrids (F_2) from 21 combinations of Mono-Chinese Spring \times Mil'turum 553. The hybrids consist of the following population: $2n-1 = 41$ ($\approx 74\%$), $2n = 42$ ($\approx 23\%$) and $2n-2 = 40$ ($\approx 3\%$).

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5. First generation disomic hybrid from Chinese Spring \times Mil'turum 553.
6. Second generation disomic hybrid from Chinese Spring \times Mil'turum 553.

The experiment was conducted in 1971 with 8-fold replication and in 1972 with 4-fold repetition. The plots were double-rowed in 1971 and triple-rowed in 1972. Row length was 200 cm. The seeds were sown with a hand sower with 4 cm distance between rows and 10 cm distance in the row. Structural analysis was performed for each plant. Grain weight per head was determined by dividing grain weight per plant by the number of productive spikes. The number of plants analyzed ranged from 51 to 170 (with a mean of 115 per hybrid).

The vegetation conditions differed substantially in the two years, particularly with respect to watering and temperature. In 1971, precipitation in June was 18 mm above the perennial norm and in July it was 50 mm less than this norm. Mean air temperature corresponded to the perennial mean in June, it was 1.4° higher in July and 0.8° lower in August. The relatively high temperature and minimal rainfall in July created unfavorable conditions during the wheat heading and flowering stages. In 1972, rainfall in June was 31 mm higher than the perennial norm, it was 18 mm more in August and 13 mm less than the norm in July. Air temperature was 1.1° lower than the perennial mean in June, 1.9° lower in July and 1.5° lower in August. The significant heat deficiency with good rainfall created poor conditions in 1972 during plumping and maturation of grain.

Experimental Data and Discussion

Variance analysis shows that the differences between F_1 and F_2 hybrids, with respect to kernel weight per head, are reliable with a high degree of probability ($P < 0.001$) in both 1971 and 1972 (Table 1). Correlation analysis revealed that there is not a very close link between generations according to grain weight per spike: $r = +0.772$ ($P < 0.001$) in 1971 and $r = +0.520$ ($P < 0.05$) in 1972. This is probably attributable to the fact that F_1 and F_2 of each hybrid differ in chromosomal constitution. In F_1 of the monosomic hybrid part of the genotypes ($\approx 25\%$) has the same chromosomal constitution as the disomic hybrid, whereas disomic plants in the F_2 population differ from the disomic hybrid. Moreover, some of the F_2 plants ($\approx 3\%$) have a nullisomic structure. The differences in chromosomal constitution combined with recombination of genes against this background probably lead to substantial changes in genotype reaction in F_1 and F_2 to environmental conditions.

The mild correlation between hybrids according to year, both in F_1 ($r = +0.442$) and F_2 ($r = +0.222$) is indicative of significant genotype \times environment interaction.

Table 2 lists data on grain weight per spike for monosomic and disomic hybrids (F_1 and F_2) and the original cultivars. In 1972, kernel weight

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per head was higher on the whole in the experiment than in 1971. In second generation hybrids, grain weight is lower on the average than in the first generation. In 1971, the initial cultivars differed appreciably; the differences between cultivars were unreliable in 1971. There was more marked fluctuation in different years in kernel weight for Chinese Spring than Mil'turum 553. Under the less favorable conditions (1971), monosomic F_1 hybrids were close to Mil'turum 553, while F_2 occupied an intermediate place between the cultivars. Under these conditions, the disomic F_2 hybrid was closer to Mil'turum 553. In 1972, the initial cultivars did not differ from one another, while monosomic F_1 hybrids were generally closer to Chinese Spring. There was manifestation in the disomic F_1 hybrid of the heterosis effect (7%); however it was statistically unreliable. In the disomic F_2 hybrid there was a reliable drop in kernel weight, as compared to F_1 . This indicates that the heterosis effect is due to overdominance.

Table 1. Results of variance analysis

Source of variability	1971				1972			
	F_1		F_2		F_1		F_2	
	ms	F ^{act}	ms	F ^{act}	ms	F	ms	F ^{actual}
Hybrids	3,02	9,15	1,99	6,03	1,59	8,83	1,58	7,06
Replication + plants	0,33	—	0,33	—	0,18	—	0,22	—

*F with $P = 0,001 - 1,92$

Kernel weight per head is lower in most monosomic hybrids than in disomic ones and, while the deviations are not reliable in all instances, this is merely indicative of the inadequate sensitivity of the method used to test hybrids in the field (Table 2). The general conclusion is that a monosomic state for virtually all chromosomes in the material examined leads to reduction of head productivity. In 1971, 13 monosomic F_2 hybrids differed reliably from the F_2 disomic hybrid with respect to kernel weight per spike, and in only one instance (1B) was the monosomic hybrid superior to the disomic one. In 1972, 15 monosomic F_1 hybrids and 11 F_2 hybrids differed reliably from disomic F_1 and F_2 hybrids, and in four cases (2A, 1B, 5B, 6D) kernel weight per spike was higher in the monosomic hybrid, while in others it was lower than in the disomic hybrid.

There was marked hybrid \times environment interaction with regard to the trait studied. Head productivity in F_1 and F_2 diminished reliably in both 1971 and 1972 only in 3 hybrids that were monosomic for chromosomes 4D, 5D and 7D. In 1971, maximum effectiveness in the monosomic state was manifested for chromosomes 6A, 1B, 3B, 4B, 1D, 2D, 4D, 5D and 7D, whereas in 1972 this applied to chromosomes 2A, 5A, 7A, 5B, 3D, 4D, 5D, 6D and 7D. The obtained results clearly indicate that one cannot derive any definitive conclusions as to genetic control of a quantitative character such as kernel weight per spike on the basis of studying hybrids under the same conditions. The genetic system of control of development of quantitative

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Table 2. Kernel weight per spike, g

Hybrids and parents	1971			1972			
	F_1		$\pm d$	F_1		$\pm d$	
	\bar{x}	\bar{x}		\bar{x}	\bar{x}		
Mono 14X1553	1.02	0.88	-0.15*	1.20	-0.12*	1.19	-0.06
24X	1.36	0.98	-0.08	1.46	+0.14**	1.30	+0.17**
34X	0.86	0.85	-0.21*	1.17	-0.15**	1.12	-0.01
44X	0.98	0.90	-0.16	1.25	-0.07	1.10	-0.03
54X	1.08	0.94	-0.12	1.17	-0.15**	1.01	-0.12*
64X	1.02	0.82	-0.24**	1.37	+0.05	1.10	-0.03
74X	1.08	1.05	-0.01	1.12	-0.20***	1.02	-0.11*
For genome A	1.06	0.92	-0.14	1.25	-0.07	1.12	-0.01
Mono 18X1553	1.38	1.28	-0.22**	1.19	-0.13*	1.27	+0.14**
28X	1.24	0.97	-0.09	1.12	-0.20***	1.20	+0.07
38X	0.81	0.80	-0.26**	1.30	-0.02	0.96	-0.17**
48X	0.69	0.66	-0.40***	0.98	-0.34***	1.09	-0.04
58X	1.19	0.98	-0.08	1.12	-0.20***	1.27	-0.14**
68X	1.12	0.85	-0.21*	1.19	-0.13*	1.12	-0.01
78X	1.31	0.93	-0.13	1.20	-0.12*	1.12	-0.01
For genome B	1.11	0.92	-0.14	1.16	-0.16	1.15	+0.02
Mono 1D X1553	1.04	0.67	-0.39***	1.25	-0.07	1.21	+0.08
2D X	0.82	0.76	-0.30***	1.24	-0.08	1.14	+0.01
3D X	0.98	1.01	-0.05	1.13	-0.19**	0.93	-0.18**
4D X	0.84	0.74	-0.32***	1.07	-0.25***	1.00	-0.13*
5D X	0.74	0.78	-0.28***	0.83	-0.49***	0.89	-0.23***
6D X	1.13	0.79	-0.27**	1.24	-0.08	1.27	+0.14**
7D X	1.00	0.76	-0.30***	1.15	-0.17*	0.99	-0.14**
For genome D	0.94	0.79	-0.27	1.13	-0.19	1.06	-0.07
Ch.Spr. x1553	1.04	0.88	-0.18	1.18	-0.14	1.11	-0.02
Chinese Spring	0.60	—	—	1.23	—	—	—
1553	1.09	—	—	1.25	—	—	—
*HCP _{0.95}	—	—	0.17	—	0.11	—	0.10
**HCP _{0.99}	—	—	0.22	—	0.14	—	0.14
***HCP _{0.999}	—	—	0.28	—	0.18	—	0.19

Key: HCP) lowest appreciable difference

characters is in complex interaction with environmental conditions. Depending on the combination of environmental factors at different stages of development of an organism, there is substantial change in allelic and non-allelic gene interaction, and this, in turn, affects the nature of inheritance of a trait. Monosomic analysis revealed that head productivity is controlled by many genes localized in all chromosomes, with the exception of 4A. It is to be expected that testing hybrids under other conditions would also reveal the effect of chromosome 4A. Analysis also showed that the monosomy effect depends on the chromosomal constitutions of genotypes in F_1 and F_2 . The monosomic state (with the exception of four cases) leads to attenuation of the character, and this is indicative of the dose effect of chromosomes and additive action of genes that control the trait in question. The absence of one chromosome in most hybrid plants (75%) rules out some of the information that determines spike productivity. It is also probable that the absence of a chromosome has some adverse effect on cell metabolism and on morphological processes as a whole.

The chief cause of the monosomic state effect is that each structural element of the spike is controlled by many genes. These elements include spike length, number of spikelets, number of kernels per spike and spikelet, and kernel size. Each of these characters can also be broken down into elements,

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especially if we take into consideration physiological, biochemical and other properties. For this reason, exclusion of any chromosome (i.e., 2.38% of the genetic information) from the full set (42 chromosomes = 100%) should affect the end result of spike development and productivity.

The instances when monosomy leads to an increase in kernel weight per spike, as compared to disomy, are of special significance. Evidently, in such cases there is exclusion of genes with inhibitory effect on some elements of spike structure. In these cases too, the environment plays an important role.

On the basis of the obtained data, it is assumed that kernel weight per spike is controlled by many genes, chiefly those with additive action. The results of our 2-year study of hybrids indicate that maximum effectiveness in the monosomic state was manifested with regard to chromosomes 2A, 1B, 3B, 4B, 1D, 2D, 3D, 4D, 5D, 6D and 7D. The obtained information can be used in future genetic research involving chromosome substitution, as well as for development of breeding programs for wheat.

Conclusions

1. The monosomy of F₁ and F₂ hybrids, which were obtained from crossing monosomic lines of Chinese Spring wheat with the Siberian Mil'turum 553 cultivar, causes a decrease in kernel weight per spike, with the exception of four cases (1B in 1971, 2A, 1B, 5B and 6D in 1972), in which monosomy reliably induces an increase in kernel weight, as compared to the disomic hybrid.
2. Maximum effectiveness of monosomy was manifested in 1971 for chromosomes 6A, 1B, 3B, 4B, 1D, 2D, 4D, 5D, 6D and 7D, and in 1972 for 2A, 5A, 7A, 3D, 4D, 5D and 7D.
3. We observed significant hybrid × year interaction. There was a reliable decrease in kernel weight per head, in both 1971 and 1972, in three hybrids (F₁ and F₂) that were monosomic for chromosomes 4D, 5D and 7D.

BIBLIOGRAPHY

1. Sears, E. R. RES. BUL. MIS. AGRIC. EXPT. STAT., 572, 1954, 1-58.
2. Williams, W. "Genetic Bases and Breeding of Plants," Moscow, Kolos, 1968.
3. Elliot, F. "Plant Breeding and Cytogenetics," Moscow, Izd-vo inostr. lit. [Foreign Literature Publishing House], 1961.
4. Kuspira, I., and Unrau, I. CANAD. J. GENET. AND CYTOL., 1, 1959, 267.
5. "Cytogenetics of Wheat and Its Hybrids," Moscow, Nauka, 1971.

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6. Allan, R. E., and Vogel, O. A. CROP SCIENCE, 3, No 6, 1963, 538.
7. Tsil'ke, I. A.; Maystrenko, O. I.; and Gerasenkov, B. I. "Nauchnyye trudy SibNIISKhoza" [Scientific Works of the Siberian Scientific Research Institute of Agriculture], 4(19), 1973.
8. Tsil'ke, R. A., and Tsil'ke, I. A. GENETIKA [Genetics], 9, No 5, 1973. [485-10,657]

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CSO: 8144/0485

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UDC: 575.12:633.11

MONOSOMIC ANALYSIS OF NUMBER OF SPIKELETS PER SPIKE OF SOFT SPRING WHEAT

Moscow GENETIKA in Russian Vol 10, No 8, 1974 pp 5-10

[Article by I. A. Tsil'ke and R. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 2 Jan 74]

[Text] Introduction

The wheat head has a set of characters with breeding and taxonomic importance. Different combinations and intensity of these traits yield a wide diversity of spike shape and density and, consequently, its productivity. The accessibility and simplicity of taking measurements have enabled many researchers to study inheritance of structural elements of the spike. The more experimental data were accumulated, the more obvious it became that each spike element is controlled by many genes with different types of action and interaction.

The main information about inheritance of spike characters was obtained from hybridological analysis. Filipchenko [1] summarized his findings and the results obtained by other researchers, and he arrived at the conclusion that spike length and number of spikelets per spike of soft wheat are controlled by at least 14 genes (allelic pairs), which can be divided into two groups according to their action: 1) genes that control only spike length, and 2) genes that control both spikelet number and spike length.

The polyploidy of soft wheat does not permit localization of genes by means of hybridological analysis. This became feasible only as a result of using cytogenetic methods [2].

In this article we report the results of monosomic analysis of number of spikelets per spike in a Chinese Spring × Mil'turum 553 hybrid. The results of monosomic analysis of spike density and stem length of this hybrid have been reported previously [3, 4].

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Material and Methods

The working hypothesis for the experiment and cytological methods were described in [3]. The following were used in the experiment: Chinese Spring (CS) cultivar, Mil'turum 553 (M553) cultivar, disomic CS \times M553 F₁ hybrid, disomic CS \times M553 F₂ hybrid, monosomic F₁ hybrids from 21 combinations of mono-CS \times M553, monosomic F₂ hybrids from 21 combinations of mono-CS \times M553. In 1971, the experiment was conducted in 8 replications, and in 1972 in 4. The Plots were arranged at random in the block. The plant feeding area constituted 0.04 m² (10 cm \times 40 cm). In 1971, the specimens were planted in 2-row plots and in 1972, in 3-row plots. The plots were 200 cm in length.

The vegetation conditions differed substantially in the 2 years. In 1971, conditions were favorable from germination to heading time for development of the plants; at the heading and flowering stages the plants suffered from a shortage of water in the presence of relatively high temperatures. In 1972 the plants developed with a good supply of water, but shortage of heat during the period between shooting and maturation.

At the end of the yellow-ripe stage and beginning of the full-ripe stage the plants were removed and, after drying, their structural elements were analyzed.

Results and Discussion

We submit below data on number of spikelets per spike in the original cultivars and disomic F₁ and F₂ hybrids ($\bar{x} \pm s_{\bar{x}}$):

<u>Cultivar, hybrid</u>	<u>1971</u>	<u>1972</u>
Chinese Spring	18.0 \pm 0.19	20.3 \pm 0.18
M553	19.9 \pm 0.21	20.1 \pm 0.19
F ₁ Chinese Spring \times M553	--	21.7 \pm 0.17
F ₂ Chinese Spring \times M553	21.1 \pm 0.27	21.9 \pm 0.30

Under the less favorable conditions of 1971, the cultivars differed reliably in number of spikelets per spike, whereas in 1972 the differences between cultivars were unreliable. It is known that, unlike many other quantitative traits, the number of spikelets is characterized by relative stability of expression under different conditions. However, in our experiments, this character was more pronounced in 1972 in both the cultivars and hybrids, and it was more stable in Siberian M553 than in the CS cultivar that is not adapted to the local conditions.

At first glance one would think that the original cultivars differ substantially in structural elements of the spike. After all, the differences in spikelet number were insignificant, and they were reliable only in 1971. However, as we have demonstrated [3], the cultivars studied differ

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appreciably in spike density. CS is characterized by a relatively short, firm head with slightly clavate [club] shape, while M553 is characterized by a long spike of medium density and spindle shape. The differences in density and shape of spike indicate that the original cultivars differed substantially in genes that control the number of spikelets per spike.

The first generation disomic hybrid was not studied in 1971; for this reason we shall discuss here only the data for 1972. In F_1 there was expression of a reliable heterosis effect, which constituted 7% in relation to the best parent. Apparently, the heterosis effect is unrelated to heterozygosity (overdominance), since there was no decrease in number of spikelets in F_2 , as compared to F_1 .

It is known [5-10] that there is occasional expression of an insignificant heterosis effect in F_1 with respect to number of spikelets in soft wheat. Diallele analysis revealed [11, 12] that strong inheritance is observed for this character, due mainly to the additive action of genes.

The data obtained for each monosomic F_1 and F_2 hybrid population tested under field conditions in 1971 and 1972 are indicative of the influence of different chromosomes on expression of the trait in question. The Table lists the means (\bar{x}) and deviations (d) of the mean for the monosomic population from the mean for the disomic hybrid. In order to avoid excessive figures in the table, it does not list standard mean error ($s_{\bar{x}}$) or the results of variance analysis. We shall merely indicate that the value of F (Fisher's criterion) fluctuated as a function of year and generation from 5.6 to 12.2 with a tabular value of $F = 1.9$ ($P < 0.001$). The reliability of deviations of the mean for the monosomic population from the mean for the disomic hybrid was determined on the basis of the lowest appreciable difference (HCP) and the χ^2 method.

As can be seen in the Table, monosomy generally elicited a decrease in number of spikelets per spike, as compared to disomy. In only 2 F_2 hybrids that are monosomic for chromosomes of the fifth homological group (5A and 5D) do we observe a reliable increase in number of spikelets, as compared to the disomic F_2 hybrid, and this under less favorable conditions for development of wheat plant (1971). It is known that the suppressor gene for spike density is localized in chromosome 5A of the CS cultivar. In the absence of this chromosome, the spike becomes lax, i.e., speltoid [2]. As we have demonstrated, the spike of the CS \times M55s hybrid, which is monosomic for chromosome 5A, did not differ appreciably in density from the spike of a disomic hybrid [3], but did differ substantially from it in length (our unpublished data). Elongation of the spike also led to an increase in number of spikelets.

Monosomy for chromosome 5D induced an increase in spike density [3], chiefly as a result of increase in number of spikelets, as shown by the data discussed here. Typically enough, the monosomy effect referable to chromosomes 5A and 5D is related to environmental conditions under which the hybrid plants develop.

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Number of spikelets per spike in hybrids

Hybrid	1971			1972			
	F ₁		F ₂	F ₁		F ₂	
	\bar{x}	\bar{x}		\bar{x}	sd	\bar{x}	sd
Mono-1A×M553	19.1	19.9	-1.2*	20.3	-1.4***	21.3	-0.6
" 2A×M553	20.1	20.1	-1.0*	21.4	-0.3	21.8	-0.1
" 3A×M553	18.2	20.0	-1.1*	20.5	-1.2***	20.8	-1.3***
" 4A×M553	18.8	20.3	-0.8	21.2	-0.5	21.7	-0.2
" 5A×M553	19.8	22.2	+1.1*	21.3	-0.4	21.5	-0.4
" 6A×M553	18.8	19.2	-1.9***	20.5	-1.2***	20.6	-1.3***
" 7A×M553	19.7	20.6	-0.5	20.4	-1.3***	20.1	-1.8
Mean for genome A	19.2	20.3	-0.8	20.8	-0.9	21.1	-0.8
Mono-1B×M553	18.4	19.1	-2.0***	21.4	-0.3	21.4	-0.5
" 2B×M553	21.0	21.4	+0.3	21.4	-0.3	21.8	-0.1
" 3B×M553	18.5	19.4	-1.7***	20.2	-1.5***	20.0	-1.9***
" 4B×M553	18.3	18.9	-2.2***	20.1	-1.6***	20.4	-1.5***
" 5B×M553	18.8	19.6	-1.6**	21.4	-0.3	21.5	-0.4
" 6B×M553	19.0	20.0	-1.1*	21.4	-0.3	21.4	-0.5
" 7B×M553	19.1	21.6	+0.5	20.9	-0.8**	21.3	-0.6
Mean for genome B	19.0	20.0	-1.1	21.0	-0.7	21.1	-0.8
Mono-1D×M553	19.6	19.5	-1.6***	21.4	-0.3	21.2	-0.7
" 2D×M553	18.0	20.0	-1.1**	19.5	-2.2***	19.7	-2.2***
" 3D×M553	18.5	20.0	-1.1**	20.7	-1.0***	19.7	-2.2***
" 4D×M553	18.9	19.7	-1.4**	20.4	-1.3***	20.5	-1.4***
" 5D×M553	21.4	22.1	+1.0*	21.7	0.0	21.7	-0.2
" 6D×M553	19.7	20.3	-0.8	21.2	-0.5	21.9	0.0
" 7D×M553	19.6	20.7	-0.4	21.3	-0.4	20.8	-1.1*
Mean for genome D	19.4	20.3	-0.8	20.9	-0.8	20.8	-1.1
Mean for all hybr.	19.2	20.2	-0.0	20.9	-0.8	21.0	-0.9

Reliable with: * P<0.05; ** P<0.01; *** P<0.001.

In 1971, the number of spikelets in 13 F₂ hybrids, monosomic for chromosomes 1A, 2A, 3A, 6A, 1B, 3B, 4B, 5B, 6B, 1D, 2D, 3D and 4D, was reliably lower than in the disomic F₂ hybrid. In 1972, the number of spikelets was reliably lower in 10 F₁ hybrids, monosomic for chromosomes 1A, 3A, 6A, 7A, 3B, 4B, 7B, 2D, 3D and 4D, and in 8 F₂ hybrids, monosomic for chromosomes 3A, 6A, 3B, 4B, 2D, 3D, 4D and 7D, as compared to disomic F₁ and F₂ hybrids. Under the more favorable conditions in 1972, the correlation [conjugation] between F₁ and F₂ hybrids is considerably greater ($r = 0.806$; $P < 0.001$) than under less favorable growing conditions ($r = 0.576$; $P < 0.01$). The significant differences in reactions of monosomic populations as related to generation are apparently due to the fact that in F₂ there is superposition of variability induced by gene recombination over the monosomy effect.

The data obtained from correlation analysis indicate that there is higher "hybrid--year" interaction in F₂ ($r = 0.375$) than in F₁ ($r = 0.634$). The stronger interaction in F₂ is probably due to the fact that, in this generation, there is segregation of plants with nullisomic constitution, which has an appreciable influence on mean value of the trait in the F₂ monosomic population.

The obtained results indicate that studies of monosomic populations under identical conditions are insufficient by far in order to obtain reliable information about the effect of monosomy on phenotypic expression of a quantitative character. We see that similar effects under different

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conditions, i.e., decrease in number of spikelets per spike as compared to disomic hybrids, were obtained in only 7 F_1 and F_2 hybrids that are monosomic for chromosomes 3A, 6A, 3B, 4B, 2D, 3D and 4D. We were impressed by the fact that 5 of the 7 monosomic hybrids are referable to 2 homological groups: 3 to the 3d group (3A, 3B, 3D) and 2 to the 4th (4B, 4D).

The report of Ausemus et al. [13] does not state how many or which chromosomes control the number of spikelets per spike, but does indicate that spike density is determined by all chromosomes, with the exception of 2B, 4D, 5A and 5D, while spike length is controlled by all but 1B, 5A and 6D. But, since spike length and density are closely related to number of spikelets, it may be assumed that this character is also controlled by most, if not all, chromosomes. The results of monosomic analysis we have discussed here are referable to only one hybrid combination, but they indicate that all chromosomes, with the exception of 4A, 2B and 6D, affect the number of spikelets per spike, and the monosomy effect is strongly modified by environmental conditions.

It should be noted that, with all their importance, the results of monosomic analysis of quantitative traits provide only preliminary information about the localization of genes in specific chromosomes. The question of direct link between phenotypic effects of monosomy and genes of a specific chromosome remains open. The demonstrated phenotypic effects on expression of a quantitative character are apparently related not only to the absence of genes controlling this character, but the sequelae that occur upon expression of genetic information of the cell as a result of exclusion of an entire chromosome carrying a significant part of the nuclear information. The latter may be indirectly related to the function of the nucleoplasmic complex responsible for expression of all of the genotype information. Hence, the phenotypic effects in monosomic plants should be attributed primarily to the missing chromosome and the changes that arise in function of the nucleoplasmic complex as a result of absence of an entire chromosome. Lines with substituted chromosomes are the most suitable for stricter proof of the link between phenotypic effects and genes.

Conclusions

A study was made of 21 hybrid F_1 and F_2 combinations, obtained as a result of crossing monosomic Chinese Spring cultivar with a Siberian soft wheat cultivar, Mil'turum 553, as compared to disomic F_1 and F_2 CS \times M553 hybrids and original cultivars CS and M553, under field conditions in 1971 and 1972. With the exception of 4A, 2B and 6D, all chromosomes in a monosomic state influence phenotypic expression of the "spikelets per spike" character.

Similar effects were obtained under different conditions for 7 F_1 and F_2 hybrids monosomic for chromosomes 3A, 6A, 3B, 4B, 2D, 3D and 4D, and the number of spikelets per spike in these hybrids diminished reliably, as compared to disomic F_1 and F_2 hybrids.

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It was shown that the effect of monosomy on expression of the character is considerably modified by environmental conditions.

There is 1 table, and bibliography lists 13 items.

BIBLIOGRAPHY

1. Filipchenko, Yu. A. "Genetics of Soft Wheats," Moscow--Leningrad, Sel'khozgiz, 1934, p 261.
2. Sears, E. R. "The Aneuploids of Common Wheat," RES. BULL. MIS. AGRIC. EXPTL. STAT., No 572, 1, 1954.
3. Tsil'ke, R. A., and Tsil'ke, I. A. "Monosomic Analysis of Spike Density in Soft Spring Wheat," GENETIKA [Genetics], Vol 9, No 5, 1973, 5.
4. Tsil'ke, I. A.; Maystrenko, O. I.; and Gerasenkov, B. I. "Monosomic Analysis of Quantitative Characters of Soft Wheat Hybrids," "Nauchn. tr. Sib. n.-i. in-ta s.-kh." [Scientific Works of the Siberian Scientific Research Institute of Agriculture], Vol 4(19), 1973, 8.
5. Mirzinski, J., and Jankovic, M. "Manifestation of Heterosis in Some Wheat Hybrids," SAVREMENA POLJOPR. [Modern Agriculture (in Croatian)], Vol 14, No 3, 1966, 247.
6. Rusanovschi, G. "Contribution to the Study of Heterosis in Wheat," AN. INST. CERCETARI CEREALE SI PLANTE TEHN. FUNDULEA [Annals of Fundulea Research Institute for Cereals and Technical Crops (Rumanian)], Vol 34, 1967, 29.
7. Sandhu, T., and Singh, G. "Studies on Expression of Heterosis in Wheat," J. AGRIC. SCI., Vol 37, No 6, 1967, 544.
8. Dimova, R. "Heterosis in Wheat," "Nauchn. tr. Vissh. selskostop. in-t G. Dimitrov. Agron. Fak. Ser. Rasteniyevodstvo" [Scientific Works of G. Dimitrov Higher Agricultural Institute, Agronomic Faculty, Series on Plant Growing (Bulgarian)], Vol 19, 1968, 127.
9. Akhmedova, E. G. "Inheritance of Quantitative Characters in First Generation Hybrids Ecologically Remote From One Another in Karabakh," "Tr. In-ta genetiki i selektsii AN AzSSR" [Works of the Institute of Genetics and Breeding, Azerbaijan Academy of Sciences], Vol 6, 1970, 118.
10. Aksel, R. "Genetic Properties of Chromosomes 4A of Timstein and 7D of Thatcher Wheat Varieties With Respect to Certain Quantitative Characters," AN. ST. UNIV. IASI., Sec 2a, Vol 16, No 2, 1970, 213.

FOR OFFICIAL USE ONLY

11. Hsu, P., and Walton, P. D. "The Quantitative Inheritance in Spring Wheat of Morphological Structures Above the Flag Leaf Node," CANAD. J. GENET. AND CYTOL., Vol 12, No 4, 1970, 738.
12. Walton, P. D. "Quantitative Inheritance of Yield and Associated Factors in Spring Wheat," EUPHYTICA, Vol 21, No 3, 1972, 553.
13. Ausemus, E. R.; McNeal, F. H.; and Schmidt, J. W. "Genetics and Inheritance," in "Wheat and Wheat Improvement," Moscow, Kolos, 1970, p 519.
[485-10,657]

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UDC: 581.167:633.11

STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 1: STEM LENGTH

Moscow GENETIKA in Russian Vol 11, No 2, Feb 75 pp 14-23

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of
Agriculture, Omsk, submitted 28 May 74]

[Text] Introduction

In the last few years, much attention has been devoted to breeding for resistance to lodging in all grain crops. As a rule, this character is related to plant height. And, although a correlation between resistance to lodging and plant height is demonstrable under certain conditions, in reality resistance is a complex character that is controlled by a complicated system of genes that interact intensively with one another and the environment. The mechanical structure of a stem, its length, susceptibility to various pathogens developing in soil are the main factors that determine the extent of resistance to lodging. Nevertheless, breeding for reduction of plant height conducted both in our country and abroad has resulted largely in increasing varietal resistance to lodging. Other conditions being equal, a short stem has an advantage over a long one, because it is more resistant to lodging when exposed to torrential rains associated with strong winds. In West Siberia, such weather conditions are the chief cause of wheat lodging over enormous areas, even in clement years when a high yield is formed. The tallness of the cultivars zoned for different rayons is the chief cause of poor resistance to lodging.

When solving problems of resistance to lodging, breeders use the most diverse sources, including short-stem specimens without, however, having a clearcut idea about the nature of inheritance of stem length and its relation to other economically useful characters in different localities. The lack of genetic information on this score for the conditions prevailing in Siberia results in empiricism in work and, not infrequently, mistakes. The first attempts at using short-stem foreign wheat specimens in breeding revealed that not all sources by far are suitable for solving the above problem. Moreover, in the case of a very continental climate, when years with relatively good precipitation alternate with years of acute drought, the

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question of stem length acquires quite special significance. In years of severe drought, wheat forms such a short culm that harvesting is often made difficult. These extremes cannot be left unheeded when breeding is pursued for resistance to lodging.

Many researchers have studied inheritance of stem length [1-11]. The contradictory results obtained are attributable mainly to environmental conditions, under which studies are conducted, and complexity of inheritance of the character. It must also be noted that some of the confusion that arises in analyzing the obtained data is related to the fact that some researchers study the entire plant height, while others study stem length. While spike length does not have a substantial effect on overall plant height in the case of long-stemmed wheat, in short-stemmed wheat the spike length often constitutes 20-40% of the overall height of the plant, and this must be taken into consideration, particularly in genetic studies.

Very few studies have been pursued in Siberia with respect to inheritance of stem length. Khlystova [12] made a rather thorough survey of the literature pertaining to the use of short-stemmed cultivars in breedings, as well as inheritance of plant height in wheat, so that we do not have to make another survey. In this article, we report the results of an experimental study of stem length in spring bread [soft] wheat used in top crosses.

Material and Methods

We used as maternal parents Dwarf S₆₉₆ A-7 (Dw), IBO-3048-433 (IBO), Pitic 62 (P62), Acadia (Ac) and Gun To-may (Gt) obtained from the collection of the All-Union Institute of Plant Growing imeni N. I. Vavilov; the cultivars Saratovskaya 29 (S29) and Mil'turum 553 (M553), which are widely zoned in Siberia, served as the paternal forms (testers) (Table 1).

Hybrid seeds were obtained in 1972 under field conditions. F₁ hybrids were raised in a hothouse in the winter of 1972/73, in vegetation containers under artificial light up to the spike-forming stage; thereafter, they developed under natural light. We sowed 12 seeds for each parent and F₁ hybrid (4 grains per container). They were sown on 23 January. The containers were placed on the shelves at random. Uniform watering and addition of fertilizer were performed in all containers. Light was provided by incandescent lamps (500 W) from 0600 to 2000 hours daily. The plants were gathered and structural analysis made as the grain matured (between 25 April and 10 May).

In the field, the experiment was repeated in 4 replicas. The plots were in double rows 2 m in length. The area of plant feeding constituted 10×20 cm. For each variant (parents, F₁ and F₂) we sowed 40 seeds on the plot, a total of 160 seeds, in 4 blocks. A hand sower was used on the hothouse lot on 29 May 1973. During the period between germination and formation of shoots, the plants were dusted with "vofatoks" [metaphos--methyl parathion] against wheat flea beetles and "skrytostebel'nyye" [stem-boring?] pests. At harvesting time, 85-95% of the sprouted plants

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had survived. We only analyzed plants for which the regional effect was ruled out. In each variant, we analyzed 20 plants per block. For analysis, we measured the length of the first spike [head].

In the hothouse, the index of accuracy of the experiment ($s_{\bar{x}_0}/\bar{x}_0$) constituted 3.4 and in the field 1.0%. The low accuracy of the hothouse experiment is related to poorly controlled environmental factors (temperature, light) and the small sample ($n = 10-12$). In 1973, the meteorological conditions were beneficial for wheat development. Mean monthly air temperature was somewhat higher than the mean over a period of many years in May, June and August, and in July it was 0.4°C lower. During the vegetation period, rainfall was 31 mm above normal (225 mm in all).

Variance analysis was conducted according to Rokitskiy [13]. We determined the degree of dominance by two methods: according to Fontdevila [14] and Gustafsson and Dormling [15]. We calculated the inheritance index according to Purty and Crane [16].

Table 1. Brief description of base material

Cultivar	VIR* catalog Number	Origin of cultivar	Characteristics of cultivar according to plant height
Dwarf S ₆₉₆ A-7	45 902	Rhodesia	Dwarf
IBO-3048-433	46 224	Italy	Semidwarf
Pitic 62	45 664	Mexico	Semidwarf
Acadia	41 989	Canada	Average height
Gun To-may	44 114	China	Tall
Saratovskaya 29	--	USSR:	"
Mil'turum 553	--	Povolzh'ye Siberia	"

*VIR--All-Union Scientific Research Institute of Plant Growing.

Results and Discussion

Table 2 lists the results of variance analysis. Under field conditions, the differences are significant not only between variants, but between replicas ($P < 0.001$), although the experimental plot was relatively homogeneous in topography and ground cover. Apparently, even insignificant differences in cultivation conditions attributable to nutrition and water conditions in different blocks affect the length of the stem. There is also statistically reliable variant replica interaction ($P < 0.01$). It is assumed that interaction is due chiefly to effects appearing as a result of raising in the same block specimens that differ appreciably in plant height. Such effects may arise when plots with dwarf and tall plants are adjacent to one another.

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Table 2. Results of variance analysis

Source of variability	Field			Hothouse		
	d_f	ms	F	d_f	ms	F
Variants (factor A)	26	24 048.12	330.93 **	10	3415.88	42.18 *
Replicas (factor B)	3	1435.00	20.00 **	2	23.00	0.28
AxB interaction	78	187.77	2.74 *	32	60.34	0.74
Random deviations	2052	68.48	—	133	80.88	—

Reliable with * $P < 0.01$; ** $P < 0.001$.

In the hothouse, there were reliable differences only between variants; however, on the whole, random variability is higher there than in the field.

Table 3 lists data on stem length of parents and hybrids. A shorter stem was formed in the hothouse than in the field: the stem is 17.62 cm shorter in the parents and 24.81 cm shorter in F hybrids. Maternal plants differed substantially in stem length, both in the field and hothouse. We failed to demonstrate differences between IBO and P62 cultivars in the field. In dwarf cultivar Dw, the stem was 2.7 times shorter in the field than in the long-stemmed Gt cultivar and 2.5 times shorter in the hothouse. It must be noted that of the 100 short-stemmed cultivars obtained from VIR and studied for 3 years in Omsk, Dw had the shortest stem. This cultivar is also unique in that it forms a rather long spike, unlike all the rest of the studied short-stemmed specimens of common [bread] spring wheat. Differences are reliable between paternal testers only when raised in the field, but the difference is so negligible that it is impossible to apply two-tester genetic analysis proposed by Jinks et al. [17]. This analysis implies that there is maximum contrast between testers for the character studied. In essence, the testers should be extreme variants with regard to expression of the character in the top cross scheme. In our experiment, the testers were not chosen for culm length, but for a number of other economically useful characters.

Table 3. Stem [culm] length, cm ($\bar{x} \pm s_x$)

Cultivar	Field					Hothouse		
	P	$\times S_{29}$		$\times M_{553}$		P	$\times S_{29}$	$\times M_{553}$
		F ₁	F ₂	F ₁	F ₂		F ₁	F ₂
Dw	44.06 ± 0.43	81.61 ± 0.53	74.60 ± 1.77	80.89 ± 0.58	83.89 ± 2.78	38.91 ± 0.93	59.27 ± 2.31	67.50 ± 1.78
IBO	81.31 ± 0.54	101.39 ± 0.57	95.24 ± 1.14	102.80 ± 0.71	100.31 ± 1.04	57.67 ± 1.41	74.00 ± 1.48	66.00 ± 1.97
P 62	81.80 ± 0.64	103.32 ± 0.70	98.30 ± 1.21	109.68 ± 0.51	107.98 ± 1.42	66.25 ± 1.47	78.18 ± 2.50	80.00 ± 2.85
Ac	85.75 ± 0.53	111.40 ± 0.67	105.15 ± 1.06	110.70 ± 0.68	112.69 ± 0.86	75.73 ± 3.21	88.01 ± 2.90	92.35 ± 2.44
Gt	120.95 ± 0.67	118.04 ± 0.75	110.44 ± 1.08	123.05 ± 0.73	118.52 ± 1.00	98.18 ± 3.07	100.54 ± 2.61	98.00 ± 3.12
S 29	110.81 ± 0.66	—	—	—	—	98.09 ± 4.71	—	—
M 553	117.22 ± 0.83	—	—	—	—	94.30 ± 3.56	—	—
(P ₀)	93.21	103.27	97.95	107.22	105.08	75.59	80.01	80.87

On the average, F₁ hybrids have a longer stem, both in the field and hothouse, than the mean for all parents. As a rule, the stem is somewhat shorter in F₂

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hybrids than in F_1 , but the differences are not reliable in all cases. In the field, the group means (\bar{x}_0) for F_1 and F_2 hybrids involving tester S29 are reliable different from the means for hybrids F_1 and F_2 involving tester M553. However, the differences as a function of tester are not reliable for all hybrids. The means for IBO×S29, Ac×S29 F_1 and Gt×S29 F_2 hybrids did not differ reliably from the means of the same hybrids but with involvement of tester M553. In the hothouse, the differences between testers are unreliable, as are those between the means of hybrids in two tester groups. But Dw×S29 and IBO×S29 F_1 hybrids differ reliably from the corresponding hybrids that involve tester M553.

Table 4 lists the results of evaluation of dominance level, calculated by two methods. Dominance calculated according to [14] makes it possible to assess reliable deviations of the mean for hybrid F_1 from the mean between the two parents. As we see, when the plants are raised under natural conditions (in the field), the means for all F_1 hybrids differ reliably from the means between parent forms ($P < 0.001$ in 7 hybrids, $P < 0.01$ in 2 and $P < 0.05$ in 1 hybrid). Consequently, there was manifestation of dominance of the parent with the longer stem in F_1 raised in the field, and the degree of dominance was related both to the genotype of the maternal parent and the tester. In the hothouse, we observed reliable deviation of mean F_1 from the mean between parents only in three hybrids (Dw×S29, IBO×M553 and Ac×M553), and in two of these cases the deviations had a negative sign, indicating dominance of the parent with the shorter stem.

Table 4. Results of evaluation of dominance in F_1

Culti- var	Field				Hothouse			
	x S29		x M 553		x S29		x M 553	
	$D = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D' = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D' = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D' = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$	$D' = \frac{F_1 - P_{min}}{P_{max} - P_{min}} \cdot 100\%$
	cm [14]	[15]	cm [14]	[15]	cm [14]	[15]	cm [14]	[15]
Dw	3.87 **	55.0	8.95 ***	62.3	-9.23 *	34.4	0.90	51.6
IBO	5.33 ***	68.1	3.54 ***	59.8	-3.88	40.4	-9.38 *	24.4
F 62	7.02 ***	74.2	10.17 ***	78.7	-3.99	37.5	-0.28	49.0
Ac	8.12 ***	103.9	4.22 ***	69.6	1.18	55.3	7.23 *	88.0
Gt	2.76 *	77.2	3.97 ***	56.3	2.40	102.4	1.76	95.4

Reliable. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

We used the formula in [15], which had been used to study dominance and overdominance in experiments with barley in a phytotron, to determine the degree (%) of dominance. If the obtained value is 50%, it means that there is intermediate inheritance or absence of dominance, if it is over 100% it is indicative of overdominance. Obviously, these methods of estimating dominance reflect only the general nature of manifestation of the character, rather than type of action of different genes. Nevertheless, the obtained results are important from the breeding point of view.

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The degree of dominance in F_1 hybrids depends on the genotype of the maternal parent, tester and cultivation conditions. Thus, when the plants are raised in the field, hybrid $Ac \times S29$ expressed complete dominance (103.9) of the parent with the longer stem and hybrid $Ac \times M553$ presented partial dominance (69.8). In the hothouse, these hybrids presented partial (69.8) and incomplete dominance (88.9), respectively. In F_1 hybrids involving dwarf cultivar Dw , partial dominance of the parent with the long stem (55.9 and 62.3) was demonstrated in the field, whereas in the hothouse the $Dw \times S29$ hybrid presented partial dominance (39.4) of the parent with the short stem, hybrid $Dw \times M553$ having intermediate inheritance (51.6). There was expression of partial dominance of the parent with a long stem in the hybrid derived from semidwarf cultivar $IB0$ and raised in the field, and in the hothouse this applied to the parent with a short stem (40.4 and 24.4). However, it should be noted that the deviations of the F_1 hybrid from the mean between parents are not reliable in all cases when the plants are raised in the hothouse. The results on variability of dominance, including complete reversal of its direction, are consistent with the data obtained under the controlled conditions of a phytotron [15], which showed that, depending on the photoperiod and temperature, the nature of inheritance of quantitative characters in a barley hybrid changed over a wide range, from intermediate inheritance, partial and complete dominance to overdominance (floating dominance).

The experiment in question was not conducted under controlled conditions; however, the obtained results for different hybrids clearly indicate that ambient conditions have a serious influence on extent and direction of dominance. Hence, the contradictory information about inheritance of stem length, obtained by different authors and published in the literature [12], is understandable. But, apparently, this is not the only reason for the contradictory facts. Stem length is controlled by many genes with different types of action and interaction, and this complicates significantly the nature of inheritance of this character. The foregoing is confirmed by the data on distribution of plants according to stem length among parents, F_1 hybrids and the segregated F_2 generation (Table 5).

As we see, the distribution of parent and F_1 hybrid plants according to stem length is close to normal and, as a rule, is contained in 5-8 classes (at 5-cm intervals). It should be noted that Table 5 lists summary data on four replicas and, as shown by variance analysis, the differences between replications are reliable. Consequently, the modifying effect of the environment, due to the influence of the replications, increases the amplitude of variability. If the phenotypic effect of the replica is not of substantial significance to interpretation of the results of plant distribution according to stem length in genotypically relatively homogeneous parents and F_1 hybrids, these effects, which smooth the differences between genotypes and segregating F_1 generations, make it difficult to interpret the obtained data on segregation. On the other hand, the F_2 sample is too small ($n = 80$) to use the χ^2 method to prove the conformity of actual

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data with the theoretical expectations. The widest spread of variability is observed in hybrids with participation of short-stemmed cultivar Dw, regardless of tester.

Table 5. Distribution of plants according to stem length, among parents, F₁ and F₂ hybrids

Parents and hybrids	Mean size of classes, cm																			
	33	38	43	48	53	58	63	68	73	78	83	88	93	98	103	108	113	118	123	128
Dw ♀	1	8	43	25	3															
Dw × S29 : F ₁																				
Dw × M 553 : F ₁			2	4	9	5	5	4	9	23	30	16	2							
IBO ♀																				
IBO × S 29 : F ₁				2	5	5	4	4	6	1	12	6	5	5	1	1				
IBO × M 553 : F ₁																				
P 62 ♀																				
P 62 × S29 : F ₁																				
P 62 × M 553 : F ₁																				
Ac ♀																				
Ac × S29 : F ₁																				
Ac × M 553 : F ₁																				
Gt ♀																				
Gt × S29 : F ₁																				
Gt × M 553 : F ₁																				
S29 ♂																				
M 553 ♂																				

Typically enough, the hybrids involving semidwarf cultivars P62 and IBO differ substantially in nature of segregation in F₂, whereas these cultivars themselves do not differ in stem length. In hybrids derived with the participation of P62, the spread of variability in F₂ is considerably wider than in hybrids with cultivar IBO. Evidently, stem length in these two varieties is controlled by different genetic systems. In hybrids involving medium-height and tall cultivars, the distribution of F₂ phenotypes is close to normal, and this indicates that the differences between these cultivars are attributable to genes with a minimal effect.

None of the 10 hybrids presented the heterosis effect for stem length. It is assumed that dwarfism (Dw) and semidwarfism (P62, IBO) is controlled by a small number of genes with strong effect, while tallness (Ac, Gt, S29, M553) is controlled by many genes having a mild effect. But this does not indicate that stem length in short-stemmed cultivars is controlled only by genes with a high effect. The modifying action of genes with low effect cannot be ruled out in these instances either. The lack of heterosis effect in F₁ of the hybrids studied, with regard to stem length, enables us to define the heritability indices in the general sense and, on this basis, to predict the effectiveness of selection for this character in segregating generations.

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Table 6. Variances (σ^2) and heritability indices (H_b)

Culti- var	$(\sigma^2)^P$	$\times S29$			$\times M 553$		
		σ^2		H_b	σ^2		H_b
		P_1	F_1		P_1	F_1	
Dw	14.96	22.62	250.10	0.90	26.66	417.82	0.92
IBO	24.23	27.43	105.61	0.73	39.09	86.56	0.54
P 62	31.35	39.09	116.97	0.69	21.04	160.81	0.80
Ac	22.41	36.06	90.20	0.64	37.21	58.85	0.35
Ge	36.33	44.87	93.11	0.57	43.06	79.49	0.44
S29	33.11	—	—	—	—	—	—
M 553	55.54	—	—	—	—	—	—

Table 6 lists variances (σ^2) for parents, F_1 and F_2 hybrids, as well as the indices of heritability calculated with the formula proposed in [16]. On the whole, the heritability indices were rather high for all hybrids, and the highest ones were obtained for hybrids derived from dwarf cultivar Dw crossed with either tester S29 (0.90) or tester M553 (0.92). For the rest of the hybrids, the heritability indices differed appreciably, depending on the tester. Thus, the heritability index was significantly higher (0.73) for the IBO \times S29 hybrid than for IBO \times M553 (0.54); it was higher for the P62 \times M553 hybrid (0.80) than for P62 \times S29 (0.69). Analogous results were obtained for other hybrids. Probably, the genotypic environment of the tester has a substantial effect on the nature of segregation in F_2 , although phenotypically there is negligible difference in stem length between testers S29 and M553.

The heritability indices and variances of phenotypic variability of F_2 make it possible to predict the high effectiveness of selection according to stem length in segregant generations of hybrids with the participation of dwarf and semidwarf cultivars. The obtained results do not permit definite determination of the number of genes controlling stem length, although phenotypic segregation in F_2 of some hybrid combinations (P62 \times S29 P62 \times M553) is consistent with monohybrid segregation (3 long stemmed:1 short-stemmed).

Conclusions

Ten topcross hybrids raised in the field presented reliable dominance of stem length in F_1 of the parent with the longer stem. When plants are raised in the hothouse, a reliable deviation of mean F_1 from the mean between parents was demonstrated in only 3 out of 10 hybrids, and in 2 cases there was expression of dominance of the parent with the shorter stem. It was shown that the degree and direction of dominance (floating dominance) is related to the genotype of parental forms and environmental conditions.

The heritability index in the general sense ranges from 0.35 to 0.92, depending on the hybrid combination. The highest heritability indices were

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obtained in hybrids from crosses between dwarf and semidwarf specimen and long-stemmed cultivars. The nature of segregation in F₂ and heritability indices are indicative of high effectiveness of selection in segregant generations with respect to stem length.

There are 6 tables; bibliography lists 17 items.

BIBLIOGRAPHY

1. Borojevic, S. "Type of Inheritance and Heritability of Quantitative Traits in Hybrids of Different Wheat Cultivars," SAVREMENA POLJOPR. [Modern Agriculture (Croatian)], Vol 13, No 7-8, 1965, 587.
2. Borojevic, S., and Mikic, D. "Appearance and Distinctions of Dwarf Lines of Wheat Obtained by Transgressive Segregation," ARCH. POLJOPR. NAUKE [Archives of Agricultural Science (Croatian)], Vol 18, No 61, 1965, 3.
3. Powell, J. B., And Schlehuber, A. M. "Components of Height Inheritance of the Semidwarf Straw Character in Wheat Triticum Aestivum L.," CROP SCI., Vol 7, No 5, 1967, 511.
4. Piech, J., and Evans, L. E. "Inheritance of Dwarfing in Crosses of Spring Wheat Varieties," GENETICA POLON., Vol 8, No 1-2, 1967, 1.
5. Allan, R. E.; Vogel, O. A.; and Peterson, C. J. "Inheritance and Differentiation of Semidwarf Culm Length of Wheat," CROP SCI., Vol 8, No 6, 1968, 701.
6. Reddy, M. V.; Heyne, E. G.; and Liang, G. H. L. "Heritabilities and Interrelationships of Shortness and Other Agronomic Characters in F₃ and F₄ Generations of Two Wheat Crosses (Triticum aestivum L. em. Thell)," Ibid, Vol 9, No 2, 1969, 222.
7. Rehman, A. A., and Rehman, Ch. A. "Heritability and Inheritance of Plant Height, Heading Date and Grain Yield in Four Spring Wheat Crosses," Ibid, Vol 9, No 6, 1969, 760.
8. Chapman, S. R., and McNeal, F. H. "Gene Action for Yield Components and Plant Height in a Spring Wheat Cross," Ibid, Vol 11, No 3, 1971, 384.
9. Khadr, F. H. "Variability and Covariability for Plant Height, Heading Date and Seed Weight in Wheat Crosses," THEOR. AND APPL. GENET., Vol 41, No 3, 1971, 100.

FOR OFFICIAL USE ONLY

10. Reyter, B. G., and Leont'yev, S. I. "Heritability of Certain Quantitative Characters and Genetic Effect of Selection in Hybrid Populations of Spring Wheat," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1972, 44.
11. Dkhote, A. K. "Nature of Inheritance of Culm Height in Hybrids of Dwarf Wheat Cultivars," SELEKTSIYA I SEMENOVODSTVO [Breeding and Seed Growing], No 2, 1972, 34.
12. Khlystova, A. F. "Short-Stemmed Wheat," "Rasteniyevodstvo (biologicheskiye osnovy). Itogi nauki i tekhniki" [Plant Growing (biological bases). Achievements in Science and Technology], Moscow, VINITI AN SSSR [All-Union Institute of Scientific and Technical Information, USSR Academy of Sciences], Vol 2, 1973, p 95.
13. Rokitskiy, P. F. "Biological Statistics," Minsk, Vysshaya shkola, 1964, p 328.
14. Fontdevila, A. "Genotype-Temperature Interaction in Drosophila Melanogaster. II: Body Weight," GENETICS, Vol 73, No 1, 1973, 125.
15. Gustafsson, A., and Dormling, I. "Dominance and Overdominance in Phytotron Analysis of Monohybrid Barley," HEREDITAS, Vol 70, No 2, 1972, 185.
16. Purdy, J. L., and Crane, P. L. "Inheritance of Drying Rate in 'Mature' Corn (Zea mays L.)," CROP SCI., Vol 7, No 4, 1967, 294.
17. Jinks, J. L.; Perkins, J. M.; and Breese, E. L. "A General Method of Detecting Additive Dominance and Epistatic Variation for Metrical Traits," J. HEREDITY, Vol 24, No 1, 1969, 45.
[485-10,657]

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CSO: 8144/0485

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MONOSOMIC ANALYSIS OF SPIKE LENGTH IN SOFT SPRING WHEAT

Moscow GENETIKA in Russian Vol 12, No 10, 1976 pp 5-9

[Article by R. A. Tsil'ke and I. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 23 Jan 76]

[Text] Introduction

The main information about inheritance of wheat head characters was obtained from hybridological analysis. Filipchenko [1] has reported the most complete information about the nature of inheritance of spike length; he arrived at the conclusion that spike length and number of spikelets per spike of soft wheat are controlled by at least 14 genes, which can be divided into 2 groups, according to their action: 1) genes that control only spike length, and 2) genes that control both spike length and number of spikelets per spike.

Considerable work has been done in recent years dealing with the nature of inheritance of spike length [2-23], and in most cases a high degree of heritability of this character is reported [5, 14, 23]. However, it must be noted that there is marked fluctuation of the heritability coefficient, in both the general and narrow sense, depending on which parental forms are used in the crosses. Low heritability of this character is reported by Reddy et al. [16].

Walton observes, on the basis of the results of diallelic analysis, that spike length is controlled mainly by genes with additive action [20-22]. But this not rule out other effects of gene action and interaction, such as overdominance, different degrees of dominance and epistasis. Evidently, in the cases where heterosis is manifested we are dealing not only with overdominance, but complementary gene action [2, 8, 12, 17, 18]. The predominant significance of additive action of genes that control spike length is confirmed by studies indicating intermediate inheritance of this character [6, 7].

We know of very few works dealing with chromosomal localization of genes that control spike length [24]. The summary of Ausemus et al. [25] indicates that all chromosomes, excepting 2B, 2D, 1B, 5A and 6D, influence the length of the spike axis.

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In view of the fact that spike length is important to breeding, it is imperative to accumulate information about genetic control and, primarily, the influence of different chromosomes on degree of expression of this character.

In this article, we report the results of monosomic analysis of spike length in a Chinese Spring \times Mil'turum hybrid. The results of monosomic analysis of stem length, spike density, number of spikelets per spike, kernel weight per spike and duration of germination--heading period were reported elsewhere [26-30].

Material and Methods

In the experiment we used Chinese Spring (CS), Mil'turum 553 (M553), disomic F_1 and F_2 CS M553 hybrids and monosomic F_1 and F_2 hybrids from 21 combinations of mono-CS \times M553. The working hypothesis, information about base material and methods used were described previously [26-28].

Experimental Section and Discussion

We submit below data on spike length in the original cultivars and disomic F_1 and F_2 hybrids ($\bar{x} \pm s_x$, m m):

<u>Cultivars and hybrids</u>	<u>1971</u>	<u>1972</u>
CS	73.2 \pm 1.25	78.3 \pm 1.37
M553	118.8 \pm 1.58	110.2 \pm 1.73
CS \times M553 F_1	--	106.5 \pm 1.15
CS \times M553 F_2	103.8 \pm 1.51	106.2 \pm 1.62

As we see, the original cultivars differ appreciably in spike length: in 1971, the difference constituted 38.6 mm and in 1972 31.9 mm. It should be noted that this character was more stable under different vegetation conditions than other quantitative characters [26, 29, 30].

In F_1 of the disomic hybrid there was manifestation of incomplete dominance in 1972, in the direction of the parent with the longer spike (M553). In F_2 spike length was the same as in F_1 , which is indicative of additive action of genes that control spike length (see Table). Evidently, in the hybrid we studied, spike length was controlled mainly by genes with additive action, but which expressed dominance at the same time.

Spike length is one of the traits for which the effect of monosomy is the most distinctly expressed.

In 1971, 11 F_2 hybrids that were monosomic for chromosomes 3A, 5A, 2B, 3B, 4B, 5B, 6B, 1D, 3D, 4D and 5D differed reliably from the disomic F_2 hybrid; monosomy caused lengthening of the spike for only one of the chromosomes (5A), whereas it caused shortening of the spike for all the others. In 6

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monosomic hybrids (3A, 3B, 4B, 5B, 3D and 4D), the spike became shorter by more than 10 mm, as compared to the disomic hybrids.

In 1972, 14 F_1 hybrids monosomic for chromosomes 2A, 3A, 3B, 4B, 5B, 6B, 7B, 1D, 2D, 3D, 4D, 5D, 6D and 7D, and 11 F_2 hybrids monosomic for chromosomes 3A, 5A, 3B, 4B, 5B, 1D, 2D, 3D, 4D, 5D and 6D differed reliably from the control. Typically enough, monosomy induced reliable increase in spike length, in both F_1 and F_2 , in two hybrids (1D and 6D).

Hybrid spike length, mm

Hybrid	1971			1972			
	P_1		F_1	P_1		P_2	
	\bar{x}	$\pm d$		\bar{x}	$\pm d$	\bar{x}	$\pm d$
Mono-CS 1A x M 553	103.1	99.0	-4.8	107.0	+0.5	108.4	+2.2
" " 2A x M 553	102.2	99.6	-4.2	103.2	-3.3 *	107.0	+6.8
" " 3A x M 553	88.2	92.8	-11.0 ***	93.2	-13.3 ***	97.4	-8.8
" " 4A x M 553	100.0	102.0	-1.8	100.2	+2.7	107.0	+6.8
" " 5A x M 553	105.7	110.2	+6.4 *	107.0	+0.5	101.2	-5.0 *
" " 6A x M 553	101.4	101.1	-2.7	105.8	-0.7	104.0	-1.6
" " 7A x M 553	100.9	102.6	-1.2	104.5	-2.0	102.4	-3.8
Mean for genome A	100.2	101.0	-2.8	104.3	-2.2	104.0	-2.2
Mono-CS 1B x M 553	100.1	99.0	-4.2	100.0	+2.4	105.0	-1.2
" " 2B x M 553	103.1	97.8	-6.0 *	104.5	-2.0	107.0	+0.8
" " 3B x M 553	93.1	92.5	-11.3 ***	98.0	-8.5 ***	98.3	-7.0 ***
" " 4B x M 553	85.5	87.5	-10.3 ***	91.4	-15.1 ***	96.3	-7.0 ***
" " 5B x M 553	92.7	93.7	-10.1 ***	94.0	-11.0 ***	101.0	-5.2 ***
" " 6B x M 553	93.7	94.1	-0.7 ***	100.7	-5.8 ***	104.1	-2.1
" " 7B x M 553	97.4	103.7	-0.1	102.8	-3.7 *	106.9	+0.7
Mean for genome B	95.4	95.0	-8.2	100.1	-6.4	102.9	-3.3
Mono-CS 1D x M 553	100.4	96.1	-7.7 **	111.8	+5.3 ***	111.7	+5.5 *
" " 2D x M 553	88.7	100.6	-3.2	98.0	-8.5 ***	93.0	-13.2 ***
" " 3D x M 553	87.7	91.4	-12.4 ***	93.7	-12.8 ***	89.7	-16.5 ***
" " 4D x M 553	94.1	92.0	-11.8 ***	99.2	-7.3 ***	97.7	-8.5 ***
" " 5D x M 553	93.6	94.4	-0.4 ***	93.3	-12.7 ***	95.4	-10.8 ***
" " 6D x M 553	100.9	100.4	-3.4	103.4	+2.0 *	111.6	+5.4 *
" " 7D x M 553	100.9	99.7	-4.1	101.0	-5.5 ***	105.9	-0.3
Mean for genome D	98.0	96.4	-7.4	100.9	-5.6	100.7	-5.5
Mean for all gen.	97.4	97.7	-6.1	101.8	-4.7	102.5	-3.7

* $P < 0.05$.
 ** $P < 0.01$.
 *** $P < 0.001$.

A reliable and similar effect of monosomy in different years and generations was expressed for chromosomes 3A, 3B, 3D, 4B, 4D, 5B and 5D. We were impressed by the fact that the same effect of monosomy was expressed for three chromosomes of the third homologous group and for two chromosomes in the fourth and fifth homologous groups. Such repetition of the monosomic effect in homologous groups apparently shows that the genes have a duplicating action, due to polyploidy of the chromosome set of hexaploid wheat.

The mean values for the genomes indicate that the monoxomy effect is greater for chromosomes referable to genomes B and D.

On the basis of the obtained data, it is assumed that the main genes controlling spike length are localized in chromosomes 3A, 3B, 4B, 5B, 6B, 1D, 3D, 4D and 5D. Modifier genes are localized in the other chromosomes that expressed the monosomic effect. It was demonstrated that the magnitude of the phenotypic effect of monosomy depends on vegetation conditions and

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generation. The monosomic effect was not expressed in either 1971 or 1972 for 5 chromosomes (1A, 4A, 6A, 7A and 1B). One of these chromosomes (1B) is mentioned in [25] as the chromosome for which the monosomy effect has not yet been demonstrated with regard to the character in question. In addition, it should be noted that two chromosomes (5A and 6D) were demonstrated in addition to those known previously [25].

It is assumed that dominant genes with additive action are localized in chromosomes 3A, 3B, 4B, 5B, 6B, 2D, 3D, 4D and 5D, since loss of one homologue of these chromosomes causes shortening of the spike in monosomic plants. The instances where monosomic hybrid populations (5A, 1D and 6D) form a longer spike than the disomic hybrid are apparently indicative of the presence of dominant genes in the relevant chromosomes, which shorten the spike, and for this reason loss thereof causes elongation of the spike in monosomic plants. The effects of these genes are very markedly modified by environmental conditions.

The difference in direction of action of the monosomic effect, depending on vegetation conditions, is attributable, in our opinion, to the great sensitivity of plants with monosomic constitution to different environmental factors in ontogenesis.

We should call attention to the fact that none of the monosomic hybrids studied presented a reliable superiority to the paternal parent, M553 cultivar, with respect to spike length.

Monosomic analysis revealed that the action and interaction of genes localized in the chromosomes of two cultivars differing markedly in spike length create a complex phenotypic expression of the character in hybrid populations.

Conclusions

The effect of monosomy on spike length was manifested in F_2 for 11 chromosomes in 1971, in F_1 for 14 chromosomes and in F_2 for 11 chromosomes in 1972. In three cases (5A in 1971, 1D and 6D in 1972) monosomy caused elongation of the spike and in all others, shortening.

The similar and reliable effect of monosomy in the 2 years and generations, in the direction of shortening of the spike, was manifested for chromosomes 3A, 3B, 3D, 4B, 4D, 5B and 5D.

In addition to previously known chromosomes, we demonstrated the influence of chromosomes 5A and 6D, in which the genes controlling spike length are probably localized.

It was demonstrated that the effect of monosomy on expression of the character is significantly modified by environmental conditions.

There is 1 table; bibliography lists 30 items.

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BIBLIOGRAPHY

1. Filipchenko, Yu. A. "Genetics of Soft Wheat," Moscow--Leningrad, OGIZ [Association of State Publishing Houses], Sel'khozgiz, 1934.
2. Akhmedova, E. G. "Inheritance of Quantitative Characters by First Generation Ecologically Remote Hybrids in Karabakh," "Tr. In-ta genetiki i selektsii AN AzSSR" [Works of the Institute of Genetics and Breeding, Azerbaijan Academy of Sciences], Vol 6, 1970, 118.
3. Lubnin, A. N. "Heterosis and Inheritance of Principal Breeding Characters in F₁ From Crosses Between Certain Winter Wheat Cultivars," "Byul. Vses. n.-i. in-ta rasteniyevodstva imeni N. I. Vavilova" [Bulletin of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov], No 32, 1973, 10.
4. Orlyuk, A. P. "Heritability and Correlation Between Plant Height and Productivity Characters in Winter Wheat Hybrids," in "Nauchnyye trudy po sel'skokhozyaystvennoy biologii" [Scientific Works on Agricultural Biology], Odessa, All-Union Breeding and Genetics Institute, 1972, p 35.
5. Rachinski, T. "Inheritance of Stem Height and Spike Productivity in Intervarietal Hybrids of Common Wheat," GENETIKA I SELEKTSIYA [Genetics and Breeding (in Bulgarian)] (NRB), Vol 4, No 6, 1971, 369.
6. Sinitsyna, S. M. "Inheritance of Spike Length in Soft Wheat," "Zap. Leningr. s.-kh. in-ta" [Notes of the Leningrad Agricultural Institute], Vol 124, No 1, 1968, 14.
7. Tsil'ke, R. A. "Variability of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIBIRSKIY VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1974, 31.
8. Aksel, R. "Genetic Properties of Chromosomes 4A of Timstein and 7D of Thatcher Wheat Varieties With Respect to Certain Quantitative Characters," AN. STI. UNIV. JASI, Sec 20, Vol 16, No 2, 1970, 213.
9. Borojevic, S. "Type of Inheritance and Heritability of Quantitative Traits in Hybrids of Different Wheat Cultivars," SAVR. POLJOPR. [Modern Agriculture (in Croatian)], Vol 13, No 7-8, 1965, 587.
10. Hsu, P., and Walton, P. D. "The Quantitative Inheritance in Spring Wheat of Morphological Structures Above the Flag Leaf Node," CANAD. J. GENET. AND CYTOL., Vol 12, No 4, 1970, 738.
11. Idem, "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54.

FOR OFFICIAL USE ONLY

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12. Jankovic, M. "Inheritance of Stem Length and Number of Kernels in Wheat Spike," SAVR. POLJOPR., Vol 17, No 7-8, 1969, 781.
13. Khadr, F. H.; Ismail, A. M.; and Morsy, M. S. "Heritabilities of Quantitative Traits Estimated by Different Methods in Generations of Wheat Crosses," EGYPT. J. GENET. AND CYTOL., Vol 1, No 2, 1972, 263.
14. Mihaljev, J. "Investigation of Heritability of Quantitative Properties Related to Yield of Certain Wheat Cultivars," SAVR. POLJOPR., Vol 16, No 1, 1968, 47.
15. Powell, B., and Schlehuder, A. M. "Components of Height Inheritance of the Semidwarf Straw Character in Wheat Triticum aestivum L.," CROP SCI., Vol 7, No 5, 1967, 511.
16. Reddy, M. V.; Heyne, E. G.; and Liang, G. H. L. "Heritabilities and Interrelationships of Shortness and Other Agronomic Characters in F₃ and F₄ Generations of Two Wheat Crosses (Triticum aestivum L. em Thell.)," Ibid, Vol 9, No 2, 1969, 222.
17. Rusanovschi, G. "Contribution to the Study of Heterosis in Wheat," "An. Inst. Cercetari Cereale si Plante Tehn. Fundulea [Annals of Fundulea Research Institute for Cereals and Technical Crops (in Rumanian)], Vol 34, 1967, 29.
18. Sandhu, T. S., and Singh, G. "Studies on Expression of Heterosis in Wheat," INDIAN J. AGRIC. SCI., Vol 37, No 6, 544, 1967.
19. Tikka, S. B. S.; Jaimini, S. N.; and Goyal, S. N. "Variability Studies in Wheat Under 'Barani' Conditions," SCI. AND CULT., Vol 39, No 3, 1973, 129.
20. Walton, P. D. "Inheritance of Morphological Characters Associated With Yield in Spring Wheat," CANAD. J. PLANT SCI., Vol 49, No 5, 1969, 587.
21. Walton, P. D. "The Use of Factor Analysis in Determining Characters for Yield Selection in Wheat," EUPHYTICA, Vol 20, No 3, 1971, 416.
22. Idem, "Quantitative Inheritance of Yield and Associated Factors in Spring Wheat," Ibid, Vol 21, No 3, 1972, 553.
23. Zonic, J., and Jovanovic, B. "Heritability and Correlations of Some Components of Yield in Two Wheat Hybrids," "Eucarpia Proc. Meet. Sec. Cereals and Physiol., Dijon, 1970," Dijon, 1971, p 365.
24. Aksel, R., and Kuspira, J. "Quantitative Genetic Analysis of Characters in Wheat Using Crosses of Chromosome Substitution Lines (Experimental Results)," GENETICS, Vol 58, No 3, 1968, 461.

FOR OFFICIAL USE ONLY

25. Ausemus, E. R.; McNeal, F. H.; Schmidt, J. W. "Genetics and Inheritance," in "Wheat and Wheat Improvement," Moscow, Kolos, 1970, p 250.
26. Tsil'ke, I. A.; Maystrenko, O. I.; and Gerasenkov, B. I. "Monosomic Analysis of Quantitative Characters in Soft Wheat Hybrids," "Nauchn. tr. Sibirskogo n.-i. in-ta s. kh. [Scientific Works of the Siberian Scientific Research Institute of Agriculture], Vol 4(19), 1973, 8.
27. Tsil'ke, R. A., and Tsil'ke, I. A. "Monosomic Analysis of Spike Density in Soft Spring Wheat," GENETIKA [Genetics], Vol 9, No 5, 1973, 5.
28. Tsil'ke, I. A., and Tsil'ke, R. A. "Monosomic Analysis of Number of Spikelets per Spike in Soft Spring Wheat," Ibid, Vol 10, No 9, 1974, 5.
29. Tsil'ke, I. A. "Monosomic Analysis of Kernel Weight per Spike of Soft Spring Wheat," IZV. SO AN SSSR. SER. BIOL. NAUK [News of the Siberian Department of the USSR Academy of Sciences. Biological Sciences Series], Vyp 3, No 15, 1974, 85.
30. Idem, "Monosomic Analysis of Duration of Germination--Heading Period for Soft Wheat," "Nauch. tr. Sibirskogo n.-i. in-ta s. kh.," Vol 21; "Rasteniyevodstvo i selektsiya sel'skokhozyaystvennykh kul'tur v Sibiri" [Plant Growing and Breeding of Agricultural Crops in Siberia], 1974, p 27.
[485-10,657]

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STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 2: DURATION OF PERIOD FROM GERMINATION TO HEADING

Moscow GENETIKA in Russian Vol 13, No 1, 1977 pp 5-14

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 3 Jun 75]

[Text] Introduction

Vavilov [1] wrote 40 years ago: "The question of vegetation period is a major section of breeding, since it is inseparably linked with many properties. Extension or shortening of the vegetation period is associated with a change in plant chemistry, its attitude toward diseases, and not infrequently the very image of the plant changes. We expect maximum practical advances in this field in the next few years.... There has virtually been no development of genetics of the vegetation period."

When studying inheritance of duration of interphase periods, the researcher encounters methodological difficulties. It is known that information obtained from experiments conducted under natural conditions is of primary importance to the solution of breeding problems. However, the numerous environmental factors are interwoven in such a complex manner in their effects on ontogenesis that it is quite difficult to single out the components of variability induced by different environmental or genotype factors. Since genetic analysis of the vegetation period is conducted on hybrids derived from crosses between parents differing in rate of development, various conditions are formed in the course of raising the plants related to time, for the original parents, F_1 and F_2 hybrids. Morphogenesis of structural characters is closely linked with the rate of development and environmental conditions; for this reason, the genotypes of the segregant generation, which differ in duration of interphase periods, are submitted to different conditions, and this affects formation of economically useful characters and, consequently, the nature of inheritance thereof.

In view of the fact that it is technically difficult to define the maturation phases of different plants, it is more convenient to study the duration of the germination--heading period [heading date], which is closely related

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to overall duration of the vegetation period. Investigation of the nature of inheritance of duration of different interphase stages and the vegetation period as a whole using methods of hybridological analysis revealed that these characters are controlled by many genes with different types of action and interaction [2-12]. Crumpacker and Allard [7], Hsu and Walton [8, 11], who studied diallelic hybrids, established that heading is controlled mainly by genes with additive action, which manifest significant dominant and overdominant effects; there is more stable manifestation of additive action under different vegetation conditions than dominant and overdominant action. As a rule, complete and incomplete dominance, as well as overdominance, are manifested in the direction of the parent with the shorter heading date. Wehrhahn and Allard [12] developed a special system of backcrosses to identify different genes controlling heading in a hybrid obtained from crossing two wheat cultivars differing by 15 days in heading date. It was shown that the difference in heading date is controlled by 4 genes, the effect of one of these genes constituting 80% and that of the other three together 14% of total additive variance.

In this article, we submit the results of studies of inheritance of duration of germination--heading period.

Material and Methods

We used wheat cultivars from different zones as the maternal parents: Acadia (Ac), 1VO-3048-433 *1B0), Pitic 62 (P62), Dwarf S₆₉A-7 (Dw) and Gun To-may (Gt), received from the collection of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov. Saratovskaya 29 (S29) and Mil'turum 553 (M553), which are cultivars that are raised extensively in Siberia, served as the paternal parents (testers). Hybrid seeds were obtained in 1972 under field conditions. F₁ hybrids were raised in the hot-house to obtain F₂ seeds. The parents, F₁ and F₂ hybrids were studied in the field in 1973-1974. Experiments were repeated 4 times. The plots were 2 m long. The area of plant nutrition constituted 200 cm² (10×20). We planted 160 seeds (40 per block) for each parent, F₁ and F₂ hybrid; in 1974, we planted 400 seeds of each (100 per block). Sowing was done with a manual sower on 29 May in 1973 and 26 May in 1974. The plants were sprayed with vofatox (metaphos) dust against wheat flea beetles and "skrytostebel'nyye" [stem boring?] pests during the period between germination and "shooting." We recorded the heading stage for each plant, labeling the first shoot to form a head. We took for analysis only plants for which the regional effect was ruled out over the nutrition area.

The meteorological conditions were favorable for wheat development in 1973. The mean monthly air temperature was slightly higher than the perennial mean in May, June and August, and lower by 0.4°C in July. During the vegetation period the rainfall was 31 mm above the norm (a total of 225 mm). In 1974, the conditions were unfavorable. During the heading period (July) there was dry and hot weather, and this led to drastic acceleration of development. In July, there was 1.6 mm precipitation, which is 2.4% of the norm.

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Experimental Section and Discussion

Variance analysis revealed that the differences are reliable, not only between variants, but between repetitions (1974), although the experimental sector was uniform in topography and ground cover (Table 1). In 1974, there was also reliable variant \times replication interaction.

Table 1. Results of variance analysis

Source of variability	1973			1974		
	df	ms	F	df	ms	F
Variant (factor A)	27	5900,32	532,80 *	26	3976,57	278,86 *
Replication (factor B)	3	8,70	0,83	3	274,25	10,23 *
Interaction (AB)	78	14,42	1,37	78	50,06	3,55 *
Chance deviations	1895	10,51	—	5129	14,26	—

* $P < 0,001$.Table 2. Duration of germination--heading period in parents and hybrids, days ($\bar{x} \pm s_{\bar{x}}$)

Culti-var	1973					1974				
	P	S 29		M 553		P	S 29		M 553	
		F ₁	F ₂	F ₁	F ₂		F ₁	F ₂	F ₁	F ₂
Ac	39,85 \pm 0,19	39,22 \pm 0,16	40,64 \pm 0,28	45,43 \pm 0,28	49,00 \pm 0,50	39,61 \pm 0,16	40,21 \pm 0,18	40,54 \pm 0,18	44,68 \pm 0,22	46,10 \pm 0,20
1B0	56,81 \pm 0,28	39,52 \pm 0,17	41,82 \pm 0,64	46,87 \pm 0,31	53,30 \pm 0,58	48,00 \pm 0,22	41,36 \pm 0,21	42,97 \pm 0,27	48,24 \pm 0,42	51,57 \pm 0,31
P 62	61,78 \pm 0,33	39,62 \pm 0,22	41,52 \pm 0,35	47,54 \pm 0,30	59,91 \pm 0,51	47,85 \pm 0,29	40,44 \pm 0,15	43,17 \pm 0,23	48,01 \pm 0,29	52,47 \pm 0,18
Dw	62,77 \pm 0,29	38,79 \pm 0,22	41,20 \pm 0,43	47,80 \pm 0,28	57,22 \pm 0,54	48,09 \pm 0,29	40,72 \pm 0,28	42,22 \pm 0,31	48,62 \pm 0,28	51,32 \pm 0,29
Gt	63,13 \pm 0,23	42,44 \pm 0,21	43,73 \pm 0,41	50,01 \pm 0,29	61,80 \pm 0,45	46,16 \pm 0,23	42,38 \pm 0,19	43,18 \pm 0,22	49,48 \pm 0,50	53,86 \pm 0,20
S29	44,28 \pm 0,32	—	—	—	—	42,27 \pm 0,25	—	—	—	—
M 553	62,68 \pm 0,39	—	—	—	—	53,94 \pm 0,27	—	—	—	—
\bar{x}_0	55,90	39,92	41,72	47,49	56,26	46,88	41,06	42,82	47,81	51,06

Table 2 lists data on duration of the germination to heading period for the cultivars and hybrids studied. As we see, the genotype and vegetation conditions have a substantial influence on the rate of plant development. Early ripening cultivar Ac and average ripening S29 were characterized by the shortest heading date; they presented negligible differences between years. In 1973, there were insignificant differences in duration of this period in P62, Dw, Gt and M553, and in 1974 this applied to 1B0, Dw, P62 and Gt.

The difference between tester cultivars constituted 18.42 days in 1973 and 11.67 in 1974. Against the background of substantial differences between parents used in the crosses, particularly in 1973, we were impressed by the similar means for the hybrids. This period ranged from 38.79 to 42.44 days in F₁ hybrids derived from tester S29 in 1973 and 40.21 to 42.58 days in 1974, while for hybrids derived from tester M553 the figures were 45.43 to 50.01 and 44.68 to 49.48 days, respectively. For the maternal parents,

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this period ranged from 39.85 (Ac) to 63.13 days (Gt) in 1973, and from 39.61 (Ac) to 48.90 (LBO) days in 1974.

With respect to the rate of development of parents and hybrids as a whole, it should be noted that, while there were drastic differences in vegetation conditions, the F₁ hybrids presented much greater stability of development rate than the original cultivars. While the difference between group means (\bar{x}_0) constituted 9.02 days between years for the cultivars, it was 1.14 in F₁ hybrids derived from tester S29 and 0.32 for those derived from M553, and in F₂ hybrids it was 1.03 and 5.20 days, respectively.

Apparently, the phenotypic expression of the character in question depends on the nature of inheritance thereof, which is determined by the type of action and interaction of genes that control all reactions related to ontogenetic development rate. The nature of inheritance predetermines, to some extent, the rate of development under different vegetation conditions. Under favorable vegetation conditions (1973), the F₁ hybrids derived from tester S29 formed heads an average of 15 days sooner than the maternal parents. Under adverse conditions (1974), the difference dropped to 5 days and, what is very important, this was attributable to drastic acceleration of development of maternal parents. A somewhat different reaction to environmental conditions was manifested in hybrids derived from the late ripening tester M553: heading occurred an average of 7 days sooner in F₁ hybrids in 1973 and 2 days sooner than the maternal parents in 1974. We can very clearly see how environmental factors interact with the genotype.

The unfavorable vegetation conditions in 1974 at the heading stage affected primarily the late ripening varieties, accelerating their development. By virtue of their genetic structure, which is determined by the dominant action of genes, the hybrids developed at the same rate as in 1973.

A comparison of rate of development of F₁ and F₂ shows that it was negligibly retarded in hybrids involving tester S29 in F₂, whereas F₂ hybrids involving tester M553 presented appreciable slowing of development, as compared to F₁, especially under the favorable vegetation conditions in 1973.

In view of the fact that mainly complete dominance and overdominance were expressed for the character under study in F₁ hybrids, we did not evaluate the degree of dominance. Table 3 lists data on expression of the heterosis effect in F₁ hybrids. The negative values indicate that the duration of the germination--heading period is shorter in F₁ than in the parent with the shorter period. Typically enough, under favorable vegetation conditions, the heterosis effect was manifested in more hybrids than under unfavorable conditions. There was manifestation of a reliable heterosis effect in 8 hybrids in 1973 and in 2 out of 10 in 1974. Such a drastic change in nature of inheritance, when a high degree of overdominance is expressed under some conditions and dominance under others, is indicative of lability of the genetic system of control of rate of development, at least during the period between germination and heading.

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Table 3. Expression of heterosis effect in F₁ hybrids

Culti- var	1973				1974			
	S 29		M 553		S 29		M 553	
	deviat. from parent with shorter heading date							
	days	%	days	%	days	%	days	%
Ac	-0.03	1.50	5.58 *	14.00	0.60	1.51	5.07 *	12.79
1B0	-4.74 *	10.71	-9.94 *	17.50	-0.91	2.10	-0.66	1.35
P 62	-4.64 *	10.40	-14.24 *	23.05	-1.83 *	4.33	0.13	0.27
Dw	-5.17 *	12.36	-15.08 *	24.06	-1.55 *	2.67	-0.18	0.37
Gt	-1.82 *	4.12	-12.67 *	20.22	0.31	0.73	2.72 *	5.81

* P < 0.001.

Table 4. Variances σ^2 and heritability indices H_b

Culti- var	1973								1974							
	σ^2				H_b				σ^2				H_b			
	S 29		M 553		S 29		M 553		S 29		M 553		S 29		M 553	
	P	F ₁	F ₂	F ₁	P	F ₁	F ₂	F ₁	P	F ₁	F ₂	F ₁	P	F ₁	F ₂	F ₁
Ac	2.79	2.02	6.38	0.41	5.94	17.63	0.64	3.23	4.35	8.66	0.42	6.20	13.32	0.54	—	—
1B0	5.80	2.38	28.55	0.84	7.64	53.88	0.85	5.55	5.51	20.99	0.71	11.28	29.29	0.69	—	—
P 62	7.98	3.91	9.11	0.35	6.72	17.97	0.56	8.11	2.76	16.37	0.67	9.22	10.89	0.19	—	—
Dw	5.18	3.92	14.16	0.63	6.24	29.72	0.76	10.35	8.92	34.07	0.73	8.60	27.38	0.67	—	—
Gt	3.30	3.44	12.06	0.62	6.14	14.58	0.55	6.32	4.36	17.09	0.66	8.51	12.74	0.37	—	—
S 29	8.00	—	—	—	—	—	—	8.02	—	—	—	—	—	—	—	—
M 553	10.53	—	—	—	—	—	—	8.58	—	—	—	—	—	—	—	—

Table 4 lists the variances and heritability indices in the broad sense. The variances are significantly higher in F₁ hybrids derived from tester M553 than in hybrids with tester S29, with the exception of the hybrid involving Dw (1974). It should be borne in mind that very similar variance values were obtained for the testers. For this reason, the above differences in variances for F₁ hybrids are apparently related not only to differences between testers in duration of the germination--heading period, but genotypic distinctions of the testers. F₁ hybrids derived from M553 germ plasm are phenotypically less homogeneous than hybrids derived from S29 germ plasm. This could be related to the greater sensitivity of M553 plasm, which is demonstrable when it interacts with plasm of other cultivars.

The calculated heritability indices in the broad sense (H_b) give us an idea about genotypic variability of F₂ induced by segregation of genes controlling the rate of development between germination and heading. Evidently, this index cannot serve as a reliable criterion for predicting the genetic effect of selection, since a significant part of F₂ variability is induced by overdominance. This applies primarily to the results for 1973, when all hybrids except two presented the heterosis effect. Evidently, this also explains why the heritability index was lower in 1974 than in 1973 in all hybrids derived from tester M553, and we saw that there was no expression of overdominance in hybrids with this tester in 1974.

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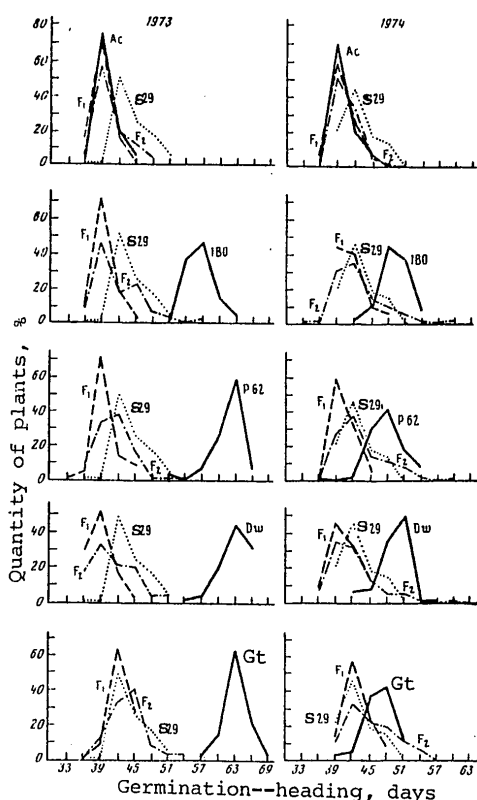


Figure 1.

Distribution of plants according to germination--heading period character in F_1 and F_2 hybrids derived from tester S29 and in their parents

curves for the late ripening parent. In 1974, the parent curves overlapped significantly for all hybrids, while the F_2 curves exceeded the limits of parent curves, which is indicative of transgressive segregation. In 180xS29 F_2 hybrids, there was segregation of transgressive recombinants, with both earlier and later heading date than in the original parents. There was segregation of recombinants with later heading date than in the late ripening parent for P62xS29, DwxS29 and GtxS29 F_2 hybrids.

The curves of plant distribution according to duration of germination--heading period provide the fullest information about parent reaction in hybrids to environmental conditions (Figures 1 and 2). The distribution of plants among parents and F_1 hybrids is close to normal; however, the curves either have pointed or bell-shaped peaks, depending on the genotype and vegetation conditions. With the exception of the early-maturing AcxS29 hybrid, all others presented appreciable differences in intensity of the trait and nature of segregation of plants in F_2 , depending on vegetation conditions. Under favorable vegetation conditions, when there was fuller expression of genetic information of each genotype, there was distinct manifestation of a difference between the parents of hybrids 180xS29, P62xS29, DwxS29 and GtxS29. In fact, the curves of parent distribution did not overlap for any of these hybrids (see Figure 1) in 1973, and the curves for F_1 hybrids were characterized by sharp peaks in all cases, which is indicative of simultaneous plant heading.

In 1973, the curves of distribution of F_2 DwxS29 and GtxS29 hybrids did not overlap, while F_2 180xS29 and P62xS29 hybrids were overlapped partially by the

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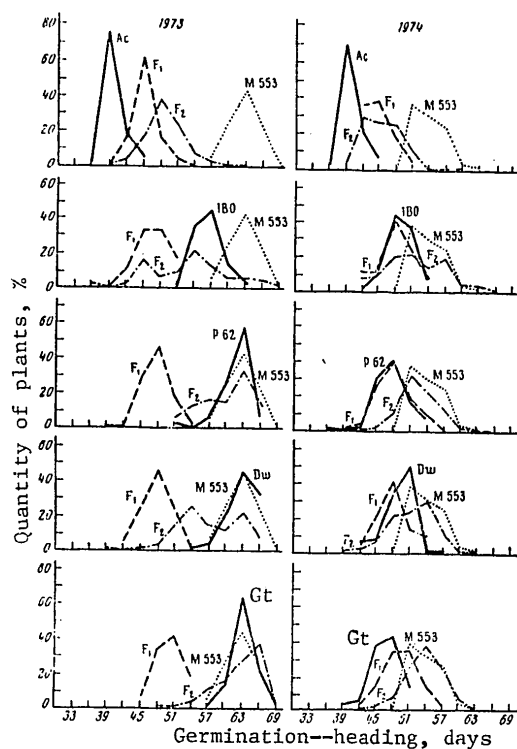


Figure 2.

Distribution of plants according to germination--heading period in F_1 and F_2 hybrids derived from tester M553 and in their parents

important to know the nature of expression and inheritance of this functionally complex character under different vegetation conditions, even within the same ecological zone. One can assess the genotypic structure of material under study only on the basis of the reaction of parents and their hybrids to specific vegetation conditions. Stability of a cultivar with regard to rate of development is particularly important from the standpoint of breeding. This is attributable to the fact that a stable variety expresses more fully the traits related to productivity. A cultivar may be classified as an intensive type if it makes utmost use of all environmental factors that are instrumental in expression of potential productivity of the genotype. Here too, the rate of development plays a very

Figure 2 illustrates the curves of plant distribution among hybrids derived from M553. In all of them, with the exception of $Ac \times M553$, the curves of the original parents overlap, either significantly or entirely. We were impressed by the fact that there was no overlapping of distribution curves for F_1 plants of $180 \times M553$, $Dw \times M553$, $Gt \times M553$ hybrids in 1973, and in hybrid $P62 \times M553$ there was partial overlapping with the curves for the original parents, whereas in 1974 the F_1 curves overlapped with those of the parents with earlier ripening and in F_2 with the ones with later ripening.

It must be noted that the vegetation conditions have a substantial effect on the nature of segregation in F_2 . Thus, the curves of distribution of $180 \times M553$ and $Dw \times M553$ F_2 hybrids were characterized by distinct presence of two peaks in 1973; in 1974, there was a mild double-peak for the $180 \times M553$ hybrid and none for the $Dw \times M553$ hybrid.

This study shows that the rate of development is subject to marked variability to a greater extent than any other trait under the influence of environmental factors; for this reason, it is extremely

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important role. If a cultivar is subject to drought at some stage or other and it reacts by marked acceleration of development, the precipitation occurring at a later time will not be utilized. But if the rate of development is retarded during a drought period, as is the case for the West Siberian ecological group of wheats, the cultivar makes more efficient use of natural and climatic conditions to augment the harvest.

With reference to the information obtained on the rate of development of local cultivars and those from other zones, as well as their hybrids, we see that all of the nonlocal cultivars, with the exception of early ripening Ac, reacted to the adverse vegetation conditions of 1974 by drastic acceleration of development. Against this background, we can clearly see the advantage of local S29 and M553 cultivars: the germination--heading period diminished by 2 days for S29 in 1974, as compared to 1973, for M553 it diminished by 9 days, whereas for LBO, P62, Dw and Gt, which are cultivars from other regions, it diminished by an average of 13 days.

In analyzing the nature of inheritance of this period in the material studied, it should be noted that this period is controlled in F_1 and F_2 hybrids mainly by genes with a dominant effect, whereas under favorable vegetation conditions there is manifestation of overdominance in the direction of accelerated development in F_1 . This type of gene action may be significant when using the heterosis effect in wheat. With the ordinary breeding programs, one must bear in mind that it is impossible to define earliest ripening by selection of phenotypes in F_2 among hybrids that present overdominance for this trait.

The obtained information makes it possible to resolve breeding problems related to selection of base material for crosses and selection of the desired recombinants in segregant hybrid populations.

The author wishes to express his sincere appreciation to S. A. Sadykova, Ye. Ya. Reger, L. K. Getman and K. Ye. Shpayder for their technical assistance with the experiment.

Conclusions

A study of 10 topcross F_1 and F_2 hybrids derived from five nonlocal cultivars used as maternal parents and two local tester cultivars revealed that the vegetation conditions have a strong influence on the nature of expression and inheritance of duration of germination--heading period.

In the presence of marked differences in vegetation conditions, the F_1 hybrids demonstrated much greater stability of rate of development than the original cultivars.

The difference between group means in different years constituted 9.02 days for the cultivars, 1.14 days for hybrids derived from average ripening tester S29 in F_2 and 0.32 day with late ripening tester M553, 1.03 and 5.2 days, respectively, in F_2 . Heading occurred 5 days earlier

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in F₁ hybrids derived from tester S29 under favorable conditions and 5 days sooner than maternal parents under unfavorable conditions; the figures for hybrids derived from tester M553 were 7 and 2 days sooner, respectively.

A reliable heterosis effect (2.65±24.06%) was manifested in 8 hybrids in 1973 and 2 out of 10 in 1974. In the other cases, the hybrids presented complete and partial dominance in the direction of the parent with the shorter germination--heading period. The index of heritability in the broad sense, H_b, ranged from 0.35 to 0.85 in 1973 and from 0.19 to 0.73 in 1974.

The curves of plant distribution revealed that there was an appreciable change in segregation in F₂ depending on vegetation conditions.

There are 4 tables and 2 illustrations; bibliography lists 12 items.

BIBLIOGRAPHY

1. Vavilov, N. I. "Genetics to Serve Socialist Agriculture," "Izbr. soch. 'Genetika i selektsiya'" [Selected works on "Genetics and Breeding"], Moscow, Kolos, 1966, p 559.
2. Karamyshev, R. M. "Inheritance of Duration of Vegetation Period in Crosses Between Ecologically Distant Forms of Soft Wheat (T. aestivum L.)," "Sb. tr. aspirantov i molodykh nauchn. sotr. Vses. n.-i. in-ta rasteniyevodstva" [Collected Works of Graduate Students and Young Scientists at the All-Union Scientific Research Institute of Plant Growing], Vol 8, No 12, 1967, 5.
3. Amaya, A. A.; Busch, R. H.; and Lebsock, K. L. "Estimates of Genetic Effects of Heading Date, Plant Height and Grain Yield in Durum Wheat," CROP SCI., Vol 12, No 4, 1972, 478.
4. Rehman, A. A., and Rehman, C. A. "Heritability and Inheritance of Plant Height, Heading Date and Grain Yield in Four Spring Wheat Crosses," Ibid, Vol 9, No 6, 1969, 760.
5. Mohamed, A. G. A. "Inheritance Studies of Some Qualitative and Quantitative Characters in Egyptian Varieties of Wheat," PRAC. EGYPT. ACAD. SCI., Vol 8, 1952, 26.
6. Bagnara, D.; Bozzini, A.; and Scarascia-Mugnozza, G. T. "Inheritance of the Duration of Developmental Phases of the Biological Cycle of Triticum Durum Desf.," GENET. AGR., Vol 25, No 1-2, 1971, 31.
7. Crumpacker, D. W., and Allard, R. W. "A Diallele Cross Analysis of Heading Date in Wheat," HILGARDIA, Vol 32, No 6, 1962, 275.

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8. Hsu, P., and Walton, P. D. "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54.
9. Khadr, F. H. "Variability and Covariability for Plant Height, Heading Date and Seed Weight in Wheat Crosses," THEOR. AND APPL. GENET., Vol 41, No 3, 1971, 100.
10. Rajinder, K.; Anand, S. C.; and Virk, D. S. "Heritability and Genetic Advance of Some Quantitative Characters in Crosses of Wheat (Triticum aestivum L.)," J. RES., Vol 9, No 4, 1972, 515.
11. Walton, P. D. "Inheritance of Morphological Characters Associated With Yield in Spring Wheat," CANAD. J. PLANT SCI., Vol 49, 1969, 587.
12. Wehrhahn, C. R., and Allard, R. W. "The Detection and Measurement of the Effects of Individual Genes Involved in the Inheritance of a Quantitative Character in Wheat," GENETICS, Vol 51, No 1, 1965, 109. [485-10,657]

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STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 3: SPIKE LENGTH

Moscow GENETIKA in Russian Vol 13, No 2, 1977 pp 197-209

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 22 Jul 75]

[Text] Introduction

The head of wheat consists of a complicated set of characters, each of which is of breeding and taxonomic significance. Different combinations and expressions of structural elements yield a wide diversity of shapes, density and, consequently, productivity of the spike. Depending on the direction of breeding and growing conditions, considerable differentiation of cultivars according to spike characters is observed in wheat. Breeders have developed unique specimens by using the natural gene pool, with regard to shape, structure and productivity of the spike, and this is indicative of the effectiveness of modern methods of upgrading wheat.

The simplicity and feasibility of measurement of structural elements of the head have made it possible for many researchers to study the nature of their inheritance. The main information concerning the nature of inheritance of spike length was obtained by the method of hybridological analysis. Special mention must be made of the classical works of Filipchenko [1] on quantitative genetics of wheat. Having summarized his own extensive experimental data and the findings of other researchers, he concluded that spike length and number of spikelets per spike of wheat are controlled by at least 14 genes (allelic pairs).

Many studies have been published in recent years that deal with the nature of inheritance of spike length [2-22], in some of which high indices of heritability of this character were obtained [4, 13, 16] and in others, low indices were found [8, 21, 22]. In addition, it is noted that indices of heritability, in both the broad and narrow sense, vary widely, depending on the base material used in the crosses and on environmental conditions under which experiments are conducted.

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Diallele analysis revealed that spike length is controlled chiefly by genes with additive action. It was also shown that the genes that control spike length manifest in some cases varying degrees of dominance, overdominance and nonallelic interaction [7, 12, 14, 15, 19]. The prevalent significance of additive action of genes in genetic control of the character under study is confirmed by studies which demonstrated intermediate inheritance [16, 22]. It is indicated in some works that an insignificant heterosis effect is expressed in F₁ hybrids [2, 9, 11].

Few experimental data have been published concerning chromosomal localization of genes that determine development of the rachis [main axis] of the spike. In the summary of Ausermus et al. [23], it is indicated that all chromosomes, with the exception of 2B, 2D, 1B, 5A and 6D, influence the length of the rachis.

Very few studies have been conducted in Siberia concerning the nature of inheritance of spike length, although such information is extremely necessary in order to upgrade breeding programs. In this article, we report the results of an experimental study of inheritance of spike length in soft spring wheat topcrosses.

Material and Methods

Nonlocal cultivars, Dwarf S₆₉₆ A-7 (Dw), IBO-3048-433 (IBO), Pitic 62 (P62), Acadia (Ac) and Gun To-may (Gt), obtained from the collection of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov, were used as maternal parents. Saratovskaya 29 (S29) and Mil'turum 553 (M553), which are cultivars that are widely grown in Siberia, served as paternal parents (testers). The base material and methods of studying parents, F₁ and F₂ hybrids under field conditions were described in detail previously [24, 25].

Experimental Section and Discussion

The results of variance analysis listed in Table 1 indicate that the differences in spike length induced by variants and replications are highly reliable ($P < 0.001$). Typically enough, in spite of relative evenness of the experimental plot with regard to topography and top soil, the conditions of different replications make a substantial contribution to the general phenotypic variability of the character. In 1973, there was also reliable variant \times replication interaction. The fact that considerable variability induced by heterogeneity of the plot and genotype \times environment interaction is demonstrable under field conditions indicates that the researcher encounters certain difficulties in genetic experiments dealing with quantitative genetics, in the presence of a certain type of gene action and interaction, as well as the contribution of an individual gene or genes to development of the character.

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Table 1. Results of variance analysis

Source of variability	1973			1974		
	df	ms	F	df	ms	F
Variant (factor A)	26	10 025.02	93.19 *	26	13 361.79	98.90 *
Replication (fact.B)	3	572.52	5.06 *	3	325.23	2.41 *
Interaction (AB)	78	226.74	2.24 *	78	189.07	1.40
Random deviations	2032	101.07	—	2083	135.11	—

* $P < 0.001$.Table 2. Spike length in hybrids and parents ($\bar{x} \pm s_x$), mm

Culti- var	1973					1974				
	P	S29		M 553		P	S29		M 553	
		F ₁	F ₂	F ₁	F ₂		F ₁	F ₂	F ₁	F ₂
Ac	68.70±0.70	80.91±0.83	79.31±1.26	86.14±0.91	90.58±1.21	67.79±0.93	83.77±0.79	81.43±0.56	92.50±1.01	94.61±0.64
IBO	73.95±0.71	79.79±0.71	79.25±1.32	93.90±0.95	88.72±1.62	71.67±0.65	85.71±0.90	84.29±0.67	92.69±1.13	95.78±0.87
Gt	96.79±0.99	90.01±0.82	88.34±1.09	107.19±0.96	99.40±1.38	87.94±0.64	92.79±0.95	88.81±0.67	99.69±1.15	96.66±0.65
P 62	106.10±1.36	88.80±1.14	87.99±1.21	104.94±0.94	102.75±1.08	91.15±0.87	93.63±0.89	91.18±0.63	102.44±1.12	98.00±0.65
Dw	106.16±1.08	94.06±0.97	93.71±1.38	112.15±1.01	109.29±1.31	92.70±0.97	88.45±1.00	92.75±0.63	106.50±1.18	107.14±0.77
S29	85.55±0.82	—	—	—	—	94.44±0.95	—	—	—	—
M 553	92.72±1.31	—	—	—	—	56.40±1.10	—	—	—	—
\bar{x}_0	90.30	86.71	85.32	100.86	98.15	84.60	88.87	87.69	98.84	98.44

Table 2 lists data on spike length in parents, F₁ and F₂ hybrids. In the maternal plants, spike length ranged from 68.70 (Ac) to 106.16 mm (Dw) in 1973 and from 67.79 to 92.70 mm in 1974. As we see, the fluctuations in the two years were more marked in late ripening cultivars Gt, P62 and Dw, than in early ripening Ac and average ripening IBO. In S29 and M553 cultivars, raised locally, this character was more stable than in the foreign cultivars characterized by an analogous rate of development. Typically enough, unlike all other cultivars, the Siberian M553 formed a longer spike under the adverse conditions of 1974 than the favorable ones of 1973.

Among hybrids derived from tester S29, spike length in F₁ ranged from 79.79 (IBO×S29) to 94.06 mm (Dw×S29) in 1973 and from 83.77 (Ac×S29) to 93.63 mm (P62×S29) in 1974; in F₂ the figures were 79.25 (IBO×S29) to 93.71 mm (Dw×S29) and 81.43 (Ac×S29) to 92.75 mm (Dw×S29), respectively. In hybrids derived from tester M553, spike length in F₁ ranged from 86.14 (Ac×M553) to 112.15 mm (Dw×M553) in 1973, and from 92.50 (Ac×M553) to 106.90 mm (Dw×M553) in 1974; in F₂, the figures were 88.72 (IBO×M553) to 109.29 mm (Dw×M553) and 94.61 (Ac×M553) to 107.14 mm (Dw×M553), respectively. It must be noted that most F₂ hybrids had a shorter spike than F₁, although the differences were usually unreliable. In 4 cases, a longer spike was formed in F₂ than in F₁; in 3 cases the differences were statistically reliable: for Ac×M553 in 1973, for Dw×S29 and IBO×M553 in 1974.

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Considering the obtained data on spike length as a whole, it should be noted that the hybrids presented greater stability each year than the cultivars. However, S29 and M553 grown locally and the foreign early ripening Ac were an exception. Thus, the difference between group means (\bar{x}_0) constituted 5.70 mm for the cultivars, 2.16 for hybrids involving tester S29 in F_1 and 2.37 in F_2 , 2.02 and 0.29 mm, respectively, for the hybrids derived from tester M553. We must call attention to the fact that the stability of expression of the character under different vegetation conditions is related to a significant extent on the rate of plant development, since expression of genetic information determining formation of the spike rachis is closely linked with occurrence of the different ontogenetic stages that are controlled by both the genotype and environment. Moreover, stability depends on adaptation of the variety to the environment in which it is raised. We refer to the adaptive reactions of the genotype and its capacity to withstand adverse environmental factors, particularly those that are extreme but briefly involved. The degree of stability of the varieties studied is related to different causes. The stability of early ripening cultivar Ac is attributable primarily to the fact that the genetically determined accelerated development of the cultivar ruled out the adverse influence of unfavorable environmental factors (inadequate rainfall and high temperatures) in July 1973, since by this time the stages of development related to formation of the main axis of the spike were already terminated in the parents. As we have already reported [25], adverse environmental factors of July 1974 induced a drastic reduction of the germination--heading period in the other foreign cultivars (IBO, P62, Dw, Gt), as a result of which there was incomplete expression of genetic information that determines development of the main axis. Thus, we see that instability of expression of the quantitative character under study in foreign cultivars is related primarily to the marked deviation of the genotype from normal with respect to rate of development, due to the lack of adaptation of these varieties to local conditions.

This correlation can be illustrated particularly well if we compare the results pertaining to local and nonlocal cultivars. There was considerably less fluctuation in duration of the germination--heading period in average ripening S29, which has been raised for a long time in Siberia, and late ripening M553 than in the foreign average ripening IBO and late ripening P62, Dw and Gt [25]. As a result of these differences in reactions of cultivars to different vegetation conditions, S29 and M553 presented much greater stability of spike length than the foreign cultivars.

Not only stability, but degree of expression of a character are important from the standpoint of breeding. While late ripening foreign cultivars Gt, P62 and Dw formed a longer spike than Siberian M553, in 1974 these cultivars were appreciably inferior to the local variety with respect to spike length. However, the means for the two years indicate that P62 and Dw form a longer spike under local conditions than M553. Hence, the breeder's task is to select recombinants from segregant hybrid P62×M553 and Dw×M553 populations that would combine the genes of P62 and Dw, which

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induce spike elongation, on the one hand, and genes of M553, which control reactions that stabilize the rate of plant development at a certain level under different vegetation conditions, on the other.

The extent and stability of expression of spike axis length in the hybrid are related not only to the nature of inheritance of this character, but nature of inheritance of duration of the stages of plant development at which the spike is established and formed. Table 3 lists the results of estimation of dominance calculated by two methods, which give us an idea about the nature of inheritance of spike length.

Table 3. Results of estimation of dominance in F_1

Culti- var	1973				1974			
	S 29		M 553		S 29		M 553	
	MM	%	MM	%	MM	%	MM	%
Ac	3.73 *	72.0	5.43 **	72.6	7.65 **	95.9	10.76 **	86.1
IBO	-1.01	39.6	9.56 **	107.0	7.85 **	109.9	8.61 **	84.7
Gt	-1.21	39.1	12.43 **	355.5	6.89 **	2.88.6	7.44 **	137.1
P 62	-7.08 **	15.4	5.53 **	91.3	5.83 **	1.46.9	8.62 **	211.4
Dw	-1.81	41.0	12.71 **	111.0	-0.12	48.0	12.30 **	371.7

* $P < 0.01$.

** $P < 0.001$.

The estimates made according to Fontdevila [26] permit determination of the reliability of deviation of mean for the F_1 hybrid (in mm) from the parent mean. As we see, these deviations are reliable in 16 cases out of 20. The formula used by Gustaffson and Dormling [27], which permits expression of degree of dominance as a percentage, is more convenient for analysis of the nature of inheritance of a character. If the estimate is 50%, it shows there is no dominance and therefore indicates an intermediate nature of inheritance. A deviation from 50% in either (plus or minus) direction describes the degree of dominance, ranging from partial to complete; if the estimate is over 100%, it is indicative of overdominance.

Upon analyzing the data in Table 3, we find, first of all, that the nature of inheritance of the character depends on the genotype of the parent forms and vegetation conditions. In hybrids involving tester S29, there was expression of intermediate inheritance of the character in 3 cases (IBO×S29, Gt×S29, Dw×S29) in 1973 and 1 case (Dw×S29) in 1974. In Ac×S29 hybrids, there was expression of incomplete dominance in both years, in the direction of the parent with the longer head; in P62×S29 hybrid, there was incomplete dominance in the direction of the parent with the shorter spike (15.4%) in 1973 and overdominance (136.9%) in 1974. There was expression of overdominance (109.9 and 238.6%) in IBO×S29 and Gt×S29 hybrids in 1974. In the hybrids involving tester M553, there was generally expression of varying degrees of dominance in the direction of the parent with the long spike and overdominance. Partial long-spike dominance was manifested in Ac×M553 (72.6%), P62×M553 (91.3%) in 1973, Ac×M553 (86.1%), IBO×M553 (84.7%) in 1974, and overdominance was demonstrated in IBO×M553, Gt×M553, Dw×M553 in 1973, and in Gt×M553, P62×M553 and Dw×M553 in 1974.

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The estimates indicate that the level and direction of dominance of spike length are unstable, and this is consistent with the data of Gustafsson and Dormling [27] obtained for a barley hybrid under the controlled conditions of a phytotron, which indicated that there was wide fluctuation of degree of dominance of quantitative characters under different conditions with regard to photoperiod and temperature.

In order to predict the effectiveness of selection in segregant generations, one must define the heterosis effect, since the superiority of a hybrid over the best parent with respect to intensity of a character induced by heterozygosity is not fixed by selection. The data in Table 3 show that overdominance was observed in 6 out of 10 F₁ hybrids, although it was not stably manifested in all of them. However, the question of whether superiority of the hybrid over the better parent is due to heterozygosity or some other action or interaction of genes remains open. Apparently, one can assume that it is induced by heterozygosity of loci controlling spike length only in those cases where heterosis, which was observed in F₁, is not manifested partially or entirely in F₂. For practical breeding purposes, it is important to determine whether the level of expression of the character of the genotype selected in the early segregant generations is retained in the strain in subsequent generations. Evidently, the earlier the generations, starting with F₂, in which the level of phenotypic expression of the character is fixed, the more reliably one can assess the selected strains and accelerate the breeding process.

Analysis of the data listed in Table 4 enables us to determine the generation and hybrid combination that one should begin with for selection for spike length. Evidently, hybrids with maximum expression of the character, in which superiority of F₁ over the best parent is retained in F₂, are of the greatest value. In such hybrids, selection will be effective, since the superiority of hybrid plants over parent plants is not related to heterozygosity. The obtained data indicate that there is manifestation of a negligible heterosis effect for spike length as a whole. This indicates that spike length in the material studied is controlled mainly by genes with additive action, which also manifest dominant and overdominant effect, depending on vegetation conditions.

In the hybrids where tester S29 participated, there was a slight, but reliable heterosis effect in Gt×S29 (5.52%) and P62×S29 (2.72%) in 1974. There was no expression of heterosis in F₂ of these hybrids. In hybrids involving tester M553, heterosis was manifested in 1973 in Gt×M553 (10.74%) and Dw×M553 (5.64%) F₁ hybrids, and it was partially retained in F₂ (2.96 and 2.94%, respectively). In 1974, heterosis was manifested in P62×M553 (6.17%) and Dw×M553 (10.79%) hybrids, and it was retained in the latter in F₂ (10.65%).

In view of the fact that overdominance makes an insignificant contribution to overall phenotypic variability of F₂, we can calculate the index of heritability in the broad sense using the formula in [28].

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Table 4. Expression of heterosis effect in F₁ and F₂ hybrids (deviation from parent with longer spike, %)

Cultivar	1973										1974									
	S 29					M 553					S 29					M 553				
	F ₁		F ₂			F ₁		F ₂			F ₁		F ₂			F ₁		F ₂		
	MM	%	MM	%		MM	%	MM	%		MM	%	MM	%		MM	%	MM	%	
Ac	-4.74 ***	5.53	-6.31 ***	7.41	-6.58 ***	7.10	-2.44	2.31	-0.67	0.79	-3.01 *	3.57	-3.99 ***	4.14	-1.88	1.05				
IBO	-3.88 ***	6.84	-6.64 ***	7.48	1.18	1.27	-4.00 ***	4.32	1.27	1.50	-0.15	0.18	-3.60 ***	3.94	-0.71	0.74				
Gt	-6.78 ***	7.00	-8.45 ***	8.74	10.40 ***	10.74	2.61 *	2.69	4.65 ***	5.52	0.87	0.88	-3.17 ***	3.28	0.17	0.17				
P 62	-17.30 ***	16.31	-20.11 ***	19.96	-1.16	1.69	-3.35 **	3.16	2.48 *	2.72	0.03	0.03	5.95 ***	6.17	1.51	1.56				
Dw	-12.10 ***	11.40	-12.45	11.73	5.99 ***	5.64	3.13 **	2.94	-4.25 **	4.58	0.05	0.05	10.41 ***	10.79	10.65 ***	11.03				

* P<0.05. ** P<0.01. *** P<0.001.

Table 5. Variances (σ^2) and indices of heritability (H_b)

Cultivar	1973							1974						
	σ^2			H_b	σ^2		H_b	σ^2			H_b	σ^2		H_b
	P	S 29			M 553			P	S 29			M 553		
		F ₁	F ₂		F ₁	F ₂			F ₁	F ₂		F ₁	F ₂	
Ac	39.81	55.52	127.48	0.60	67.45	117.59	0.34	110.91	82.36	127.19	0.23	125.54	131.29	0.02
IBO	40.50	40.50	100.39	0.69	72.21	209.90	0.62	48.92	100.39	135.69	0.22	130.80	227.51	0.19
Gt	78.42	51.29	105.82	0.37	73.20	151.81	0.40	48.77	105.13	140.43	0.37	139.86	159.86	0.25
P 62	147.61	103.28	116.89	0.12	70.03	225.46	0.53	74.39	200.88	127.44	0.23	142.90	111.39	0.11
Dw	92.37	75.22	152.92	0.51	82.41	143.23	0.31	116.77	119.79	141.80	0.16	147.64	192.01	0.27
S 29	54.18	-	-	-	-	-	-	117.36	-	-	-	-	-	-
M 553	137.70	-	-	-	-	-	-	152.43	-	-	-	-	-	-

Table 5 lists the variances (σ^2) for parent, F₁ and F₂ hybrid spike length, as well as indices of heritability in the broad sense (H_b). Variances, which reflect general phenotypic variability, fluctuate markedly according to genotype and environmental conditions. Among the parents, P62 (147.61) in 1973 and M553 (152.43) in 1974 were characterized by the highest phenotypic variability. The high variability of quantitative characters in homozygotic self-pollinating cultivars is probably attributable to two causes: genotypic heterogeneity and sensitivity of the genotype to growing conditions in the course of ontogenesis.

As shown in a study of pure-strain material, cultivar M553 is indeed characterized by rather high heterogeneity with regard to some characters [29, 30].

The high variability of foreign cultivars P62, Ac and Dw is attributable to their sensitivity to the differences in conditions in different blocks of the experimental plot. We were impressed by the fact that the variance is usually considerably higher in F₁ hybrids derived from M553 than from tester S29. These differences are related to the fact that cultivar M553 was notable for greater intrapopulation variability than S29.

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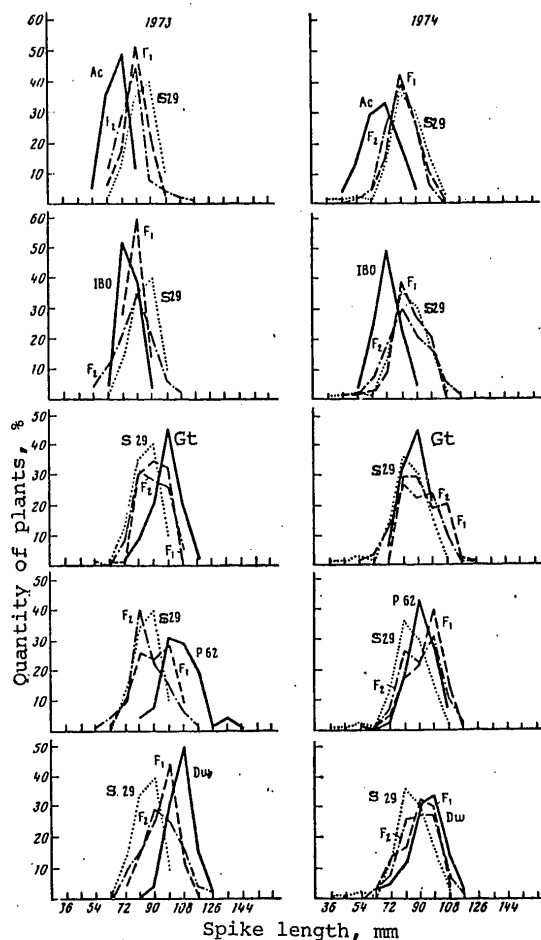


Figure 1. Distribution of plants according to "spike length" character in F_1 and F_2 hybrids (involving tester S29) and their parents

In this regard, the question arises: if a cultivar is characterized by heterogeneity, can it be included in genetic analysis? Would it not be better to isolate strains from it, breed them and then include them in the analysis? From the purely genetic point of view, such an approach is mandatory. However, from the standpoint of selection, it is important to obtain information about the nature of inheritance of varietal characters

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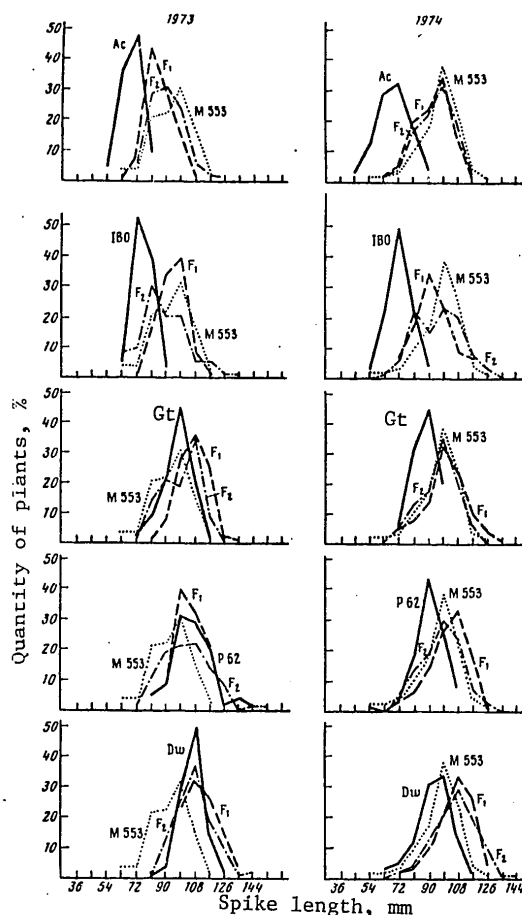


Figure 2. Distribution of plants according to "spike length" character in F_1 and F_2 hybrids (with participation of tester M553) and their parents

as a whole, i.e., in the structure that it is used in breeding programs. The heterogeneity of several characters inherent in Siberian cultivar M553 makes it superior to pure-bred cultivars. Population homeostasis of this unique variety is related expressly to heterogeneity. Hence the desire of breeders to make broader use of M553 in breeding programs is understandable, in order to impart to new varieties the characters that provide for adaptation to the rigorous conditions of Siberia.

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As can be seen from the data in Table 5, the hybrids studied differ substantially in index of heritability of spike length. The lability of the genotypes, with respect to reaction to vegetation conditions, as manifested by variance variability, resulted in marked fluctuation of the heritability index in some hybrids. For example, this index constituted 0.60 for Ac×S29 hybrids and 0.34 for Ac×M553 hybrids in 1973, 0.23 and 0.02, respectively, in 1974.

The indices for hybrids involving P62 (0.11 ± 0.53) and Dw (0.16 ± 0.51) were relatively low and unstable. They fluctuated less in different years in hybrids involving IBO (0.32 ± 0.69) and Gt (0.25 ± 0.40).

The curves of distribution according to spike length (Figures 1 and 2) provide additional information about the reactions of cultivars and hybrids to environmental conditions and nature of F₂ segregation. Analysis of the distribution curves indicates that plant distribution is close to normal, not only for parents and F₁ hybrids, but most F₂ hybrids as well. Although it should be noted that the distribution of some F₂ hybrids differed appreciably from normal. This applies to P62×S29 (see Figure 1) and IBO×M553 (see Figure 2), in which there was a double-peaked curve of distribution of F₂ plants in 1974.

In spite of these deviations, on the whole it should be concluded that spike length is controlled by a large number of genes with mild effects.

Transgressive segregation in F₂ is observed in some hybrids. Transgression was more distinct in hybrids derived from tester M553. Positive transgression was expressed in hybrid Ac×S29 in 1973 and in IBO×S29 in 1973 and 1974 (see Figure 1). Significant positive transgression, which was stable in the 2 years, was observed in hybrids IBO×M553, P62×M553 and Dw×M553 (see Figure 2).

One can predict the effectiveness of selection in segregant generations on the basis of the results of this 2-year study of parent forms and hybrids, according to nature of inheritance of the character, degree of expression of heterosis, index of heritability, phenotypic variability and nature of segregation in F₂. The highest effect of selection for spike length is expected in IBO×M553 F₂ hybrids, which are characterized by high indices of heritability, absence of heterosis in F₁, dominance of long spike trait, significant phenotypic variability of F₂ and, what is particularly important, positive transgressive segregation, as determined by complex evaluation. We expect rather effective selection of hybrids P62×M553 and Dw×M553. Thus, of the 10 hybrids studied, they were characterized by the greatest expression of the character and, moreover, considerable phenotypic variability and positive transgressive segregation in F₂. The insignificant heterotic effect manifested in F₁ of these hybrids will not have an appreciable influence on the results of selection.

Genetic analysis revealed that foreign cultivars IBO, P62 and Dw, and local cultivar M553 can serve as valuable sources of genes in breeding soft wheat for a longer spike.

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The author wishes to express his sincere gratitude to S. A. Sadykova, K. Ye. Shnayder, L. K. Getman and Ye. Ya. Reger for their technical assistance in the experiments.

Conclusions

The material studied differed substantially in nature of inheritance, reaction to vegetation conditions, index of heritability and nature of segregation in F₂.

Cultivars Gt, P62 and Dw presented less stability of spike length than the local cultivars S29 and M553.

On the average, the hybrids were more stable than the parent cultivars. The nature of inheritance of the character studied changed markedly under the influence of environmental conditions.

The estimates obtained are indicative of unstable level and direction of dominance of indices of heritability and heterosis effect. In some hybrids, there was expression of positive transgressive segregation.

Genetic analysis revealed that the most effective selection for spike length is expected in segregant F₂ and F₃ generations of IBO×M553, P62×M553 and Dw×M553 hybrids.

There are 5 tables and 2 illustrations; bibliography lists 30 items.

BIBLIOGRAPHY

1. Filipchenko, Yu. A. "Genetics of Soft Wheat," Moscow--Leningrad, OGIZ [Association of State Publishing Houses], 1934, p 262.
2. Rusanovschi, G. "Contribution to the Study of Heterosis in Wheat," "An. Inst. cercetari cereale si plante techn. (Fundulea)" [Annals of the Fundulea Research Institute for Cereals and Technical Crops (Rumanian)], Vol 34, 1967, 29.
3. Sandhu, T. S., and Singh, G. "Studies on Expression of Heterosis in Wheat," INDIAN J. AGRIC. SCI., Vol 37, No 6, 1967, 544.
4. Mihaljev, I. "Investigation of Heritability of Quantitative Properties Related to Yield of Certain Wheat Cultivars," SAVREMENA POJOPR. [Modern Agriculture (Croatian)], Vol 16, No 1, 1968, 47.
5. Aksel, R., and Kuspira, J. "Quantitative Genetic Analysis of Characters in Wheat Using Crosses of Chromosome Substitution Lines (Experimental Results)," GENETICS, Vol 58, No 3, 1968, 461.

FOR OFFICIAL USE ONLY

6. Sinitsyna, S. M. "Inheritance of Spike Length in Soft Wheat," "Zapiski Leningr. s.-kh. in-ta" [Notes of Leningrad Agricultural Institute], Vol 124, No 1, 1968, 14.
7. Walton, P. D. "Inheritance of Morphological Characters Associated With Yield in Spring Wheat," CANAD. J. PLANT SCI., Vol 49, No 5, 1969, 587.
8. Reddy, M. V.; Heyne, E. G.; and Liang, G. H. L. "Heritabilities and Interrelationships of Shortness and Other Agronomic Characters in F₃ and F₄ Generations of Two Wheat Crosses (Triticum aestivum L. em Theil)," CROP SCI., Vol 9, No 2, 1969, 222.
9. Jankovic, M. "Inheritance of Stem Length and Number of Kernels in Wheat Spike," SAVREMENA POLJOPR., Vol 17, No 7-8, 1969, 781.
10. Aksel, R. "Genetic Properties of Chromosomes 4A of Timstein and 7D of Thatcher Wheat Varieties With Respect to Certain Quantitative Characters," AN. STI. UNIV. IASI, Sec 2a, Vol 16, No 2, 1970, 213.
11. Akhmedov, E. G. "Inheritance of Quantitative Characters by Ecologically Distant First Generation Hybrids in Karabakh," "Tr. In-ta genetiki i selektsii AN AzSSR" [Works of the Institute of Genetics and Breeding, Azerbaijan Academy of Sciences], No 6, 1970, 118.
12. Hsu, P., and Walton, P. D. "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54.
13. Zonic, I., and Jovanic, B. "Heritability and Correlations of Some Components of Yield in Two Wheat Hybrids," "Eucarpia Proc. Meet. Sec. Cereals and Physiol., Dijon, 1970," Dijon, 1971, p 365.
14. Hsu, P., and Walton, P. D. "The Quantitative Inheritance in Spring Wheat of Morphological Structures Above the Flag Leaf Node," CAN. J. GENET. AND CYTOL., Vol 12, No 4, 1970, 738.
15. Walton, P. D. "The Use of Factor Analysis in Determining Characters for Yield Selection in Wheat," EUPHYTICA, Vol 20, No 3, 1971, 416.
16. Rachinski, T. "Inheritance of Culm Height and Spike Productivity in Intervarietal Soft Wheat Hybrids," GENETIKA I SELEKTSIYA (NRB) [Genetics and Breeding (Bulgarian)], Vol 4, No 6, 1971, 369.
17. Khadr, F. H.; Ismail, A. M.; and Morsy, M. S. "Heritabilities of Quantitative Traits Estimated by Different Methods in Generations of Wheat Crosses," EGYPT. J. GENET. AND CYTOL., Vol 1, No 2, 1972, 263.

FOR OFFICIAL USE ONLY

18. Orlyuk, A. P. "Heritability and Correlation Between Plant Height and Productivity Characters of Winter Wheat Hybrids," in "Nauchnyye trudy po sel'skokhozyaystvennoy biologii" [Scientific Works Dealing with Agricultural Biology], Odessa, All-Union Breeding and Genetics Institute, 1972, p 35.
19. Walton, P. D. "Quantitative Inheritance of Yield and Associated Factors in Spring Wheat," EUPHYTICA, Vol 21, No 3, 1972, 553.
20. Lubnin, A. N. "Heterosis and Inheritance of Main Breeding Characters in F₁ From Crosses Between Some Winter Wheat Cultivars," "Byul. Vses. n.-i. in-ta rasteniyevodstva imeni N. I. Vavilova" [Bulletin of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov], Vyp 32, 1973, 10.
21. Tikka, S. B. S.; Jaimini, S. N.; and Goyal, S. N. "Variability Studies in Wheat Under 'Barani' Conditions," SCI. AND CULTURE, Vol 39, No 3, 1973, 129.
22. Tsil'ke, R. A. "Variability of Nature of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIBIRSK. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1974, 31.
23. Ausemus, E. R.; McNeal, F. H.; and Schmidt, J. W. "Genetics and Inheritance," in "Wheat and Wheat Improvement," Moscow, Kolos, 1970, p 519.
24. Tsil'ke, R. A. "Study of Inheritance of Quantitative Characters of Soft Spring Wheat Topcrosses. Report 1: Stem Length," GENETIKA [Genetics], Vol 11, No 2, 1975, 14.
25. Idem, "Study of Inheritance of Quantitative Characters of Soft Spring Wheat Topcrosses. Report 2: Duration of Period From Germination to Heading," Ibid, Vol 12, No 1, 1977, 5.
26. Fontdevila, A. "Genotype-Temperature Interaction in Drosophila Melanogaster. 2: Body Weight," GENETICS, Vol 73, No 1, 1973, 125.
27. Gustafsson, A., and Dormling, I. "Dominance and Overdominance in Phytotron Analysis of Monohybrid Barley," HEREDITAS, Vol 70, No 2, 1972, 185.
28. Purdy, J. L., and Crane, P. L. "Inheritance of Drying Rate in 'Mature' Corn (Zea mays L.)," CROP. SCI., Vol 7, No 4, 1967, 294.

FOR OFFICIAL USE ONLY

29. Tsil'ke, R. A. "Genotypic and Paratypic Variability of Open Florescence of Soft Wheat," "Nauchn. trudy Sibirsk. n.-i. in-ta s. kh-va (Omsk)" [Scientific Works of the Siberian Scientific Research Institute of Agriculture (Omsk)], Vol 4, No 19, 1973, 3.
30. Idem, "Variability of Antherization Character in Soft Spring Wheat," Ibid (Novosibirsk), Vol 21, 1974, 18.
[485-10,657]

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STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 4: NUMBER OF SPIKELETS PER SPIKE

Moscow GENETIKA in Russian Vol 13, No 3, 1977 pp 396-407

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of
Agriculture, Omsk, submitted 6 Oct 75]

[Text] Introduction

The spikelet is an important element of the spike. It determines spike productivity, and for this reason the nature of expression and inheritance of spikelets per spike has been studied by many researchers [1-23]. It was shown that this is a quantitative trait characterized by polygene inheritance. It was established [2, 23] that there is intermediate inheritance with partial dominance. The F₁ hybrids present a negligible heterotic effect according to number of spikelets [3-5, 7, 10]. The indices of heritability of this character fluctuate markedly, depending on the parents used in the crosses: low indices were obtained in some studies [6, 7, 15], moderate and high ones in others [12, 14]. It was also observed that the index of heritability for one hybrid combination may change markedly, depending on plant vegetation conditions [9, 16, 23].

A study of combinative capacity of cultivars revealed that the variances of overall combinative ability are significantly higher than the variance of specific ability, which is indicative of prevalence of genes with additive action in genetic control of the character [8, 11]. Low combining capacity of cultivars according to number of spikelets per spike has been observed [17]. Diallelic analysis revealed that the variance for this character, which reflects the additive contribution of genes, constitutes most of the genotypic variability [20-22].

A survey of the literature shows that the number of spikelets is controlled by a large number of genes with different types of action and interaction. When matching base material for use in breeding programs, it is very important to have information about the nature of expression and inheritance of number of spikelets per spike, since this character is one of the chief elements determining spike productivity.

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We report here the results of an experimental study of inheritance of number of spikelets per spike of soft spring wheat topcrosses.

Material and Methods

Five foreign cultivars obtained from the collection of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov were used as maternal plants: Dwarf S₆₉₆A-7 (Dw), IBO-3048-433 (IBO), Pitic 62 (P62), Acadia (Ac) and Gun To-may (Gt). Saratovskaya 29 (S29) and Mil'turum 553 (M553), which are raised extensively in Siberia, served as the paternal parents (testers). The material was chosen in accordance with the requirements imposed by practice for a modern cultivar. Each cultivar used in the experiment is characterized by some unique characters or a set of economically useful ones: unlike most short-stemmed varieties, the Dw dwarf forms a long head with many spikelets and is resistant to brown rust [*Puccinia triticina*]; IBO is exceptionally resistant to lodging and is not stricken by powdery mildew; P62 is an intensive type of cultivar that is very responsive to high soil fertility; Ac is resistant to drought and has a high quality kernel; Gt has a productive spike and large kernel; S29 has an excellent quality of kernel and high homeostasis; M553 is exceptionally adapted to local growing conditions, which is attributable to the embryonic plasma that has undergone a long natural and artificial evolutionary process (breeding) in the steppe regions of West Siberia.

The cultivars were studied for 3-5 years in the genetic collection of the laboratory before being used in hybridization. Additional information about the base material was supplied previously [24].

Experimental Section and Discussion

The results of variance analysis, which are listed in Table 1, indicate that the differences between plants in number of spikelets per spike are attributable to the variants (parents and hybrids), replications and variant \times replication interaction, and they are highly reliable ($P < 0.001$). Typically enough, the mean squares (ms) for all components of variability are significantly higher when the plants are raised under less favorable vegetation conditions (1974).

Table 2 lists data on the number of spikelets per spike in parents, F₁ and F₂ hybrids. As compared to such quantitative characters as stem length, duration of germination--heading period and spike length, the number of spikelets per spike is characterized by the highest stability of phenotypic expression under different vegetation conditions.

In 1973, the mean number of spikelets in maternal plants ranged from 13.02 (Ac) to 20.52 (Dw) and in 1974 from 12.98 (Ac) to 19.30 (P62). We see that considerable fluctuation of mean value of the character was observed only in Dw. The difference between years constituted 3.28 spikelets for this cultivar. Even a small set of cultivars (only 7) shows that there are

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substantial differences in spikelet-forming capacity. The difference between extreme variants constituted 7.50 spikelets in 1973 and 6.32 in 1974. There was also a reliable difference between the local cultivars (testers): 1.39 spikelets in 1973 and 2.02 in 1974.

Table 1. Results of variance analysis

Source of variability	1973			1974		
	df	ma	F	df	ma	F
Variant (factor A)	26	288.58	105.32 *	26	559.48	125.10 *
Replication (fact. B)	3	12.03	4.39 *	3	67.15	15.02 *
AxB interaction	78	5.95	2.17 *	78	10.79	2.41 *
Random deviations	2052	2.74	—	5083	4.47	—

* $P < 0.001$.Table 2. Number of spikelets per spike in hybrids and parents ($\bar{x} \pm s_x$)

Hybrid cultivar	1973						1974					
	P	S 29		M 553		P	S 29		M 553		P	P
		F ₁	F ₂	F ₁	F ₂		F ₁	F ₂	F ₁	F ₂		
Ac	13.02±0.12	14.92±0.11	14.59±0.20	15.65±0.14	16.76±0.17	12.98±0.12	15.23±0.14	14.85±0.10	17.95±0.13	18.18±0.10		
IBO	17.28±0.17	15.72±0.15	16.14±0.22	18.30±0.16	17.14±0.21	16.46±0.18	16.72±0.14	16.46±0.13	18.82±0.25	18.54±0.14		
Gt	17.55±0.18	16.76±0.16	17.81±0.22	19.26±0.15	18.51±0.26	18.67±0.13	17.00±0.11	16.54±0.13	18.72±0.19	17.82±0.13		
P 62	19.91±0.20	15.71±0.15	15.88±0.21	18.66±0.12	18.78±0.23	19.30±0.15	16.21±0.15	16.56±0.12	19.51±0.19	18.12±0.11		
Dw	20.52±0.22	14.60±0.16	14.65±0.24	18.86±0.17	19.40±0.23	17.24±0.23	13.50±0.16	14.20±0.15	18.91±0.24	18.91±0.15		
S29	15.41±0.18	—	—	—	—	15.15±0.16	—	—	—	—		
M553	16.80±0.26	—	—	—	—	17.17±0.18	—	—	—	—		
F ₂	17.21	15.54	15.82	18.18	18.12	16.71	15.67	15.72	18.78	18.31		

In the hybrids derived from tester S29, the number of spikelets ranged from 14.60 to 16.76 in F₁ and from 14.59 to 17.84 in F₂, in 1973; in 1974, the range was 13.50 to 17.00 and 14.20 to 16.56, respectively. In the hybrids involving tester M553, the number of spikelets in 1973 ranged from 15.65 to 19.36 in F₁ and from 16.76 to 19.40 in F₂; in 1974, the figures were 17.95 to 19.51 and 17.82 to 18.91, respectively. Most hybrids formed just as many spikelets per spike in F₂ as in F₁. In two hybrids involving tester M553, the number of spikelets dropped reliably in F₂ as compared to F₁ (IBO×M553 in 1973 and Gt×M553 in 1974), while two other hybrids formed more spikelets per spike in F₂ than in F₁ in 1973 (Gt×S29, Ac×M553). We were impressed by the hybrid derived from crossing short-stemmed cultivar Dw with S29, in which the mean value of the character was reliably lower in both 1973 and 1974 than in the parent with the fewer spikelets (S29). However, this type of inheritance of the character was not observed when Dw was crossed with M553. It is assumed that there was expression of non-allele interaction between genes (epistasis type) controlling formation of spikelets in the spike in the Dw×S29 hybrid. It should be indicated that genetic system of control of the character functioned similarly in this hybrid under different vegetation conditions.

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As indicated by the group means (\bar{x}_0), the parents and hybrids did not differ appreciably in stability of expression of the character under different vegetation conditions. However, it should be noted that, on the average (\bar{x}_0), the number of spikelets was lower in cultivars and higher in hybrids in 1974 than in 1973.

Of course, it should be borne in mind that the years differed insignificantly with respect to conditions of establishment and formation of spikelets. This is confirmed by the fact that the first stages of organogenesis occurred in June, when watering and temperature conditions were relatively favorable both years. Nevertheless, it is important to call attention to the fact that greater variability was observed in length of the spike main axis, formed under the same conditions, than in number of spikelets. Probably, environmental conditions influence the length of the spike rachis at later stages of development as well. As it was noted, it is expressly during the heading stage that the water situation was unfavorable in 1974. The adverse environmental conditions during the heading stage, in particular the shortage of water, could not have an appreciable influence on the number of spikelets formed in the spike. True, there was one exception. There was an appreciable decrease in number of spikelets in cultivar Dw in 1974, as compared to 1973, and this was probably related to the drastic reduction of heading date observed in this cultivar in 1974. It may be assumed that, under these conditions, Dw did not express the potential capabilities of the genotype with respect to formation of structural elements of the head. Still, unlike such characters as stem and spike length, the trait under study varied much less as a function of vegetation conditions. This is important to breeding practice. It indicates that selection must be more effective for number of spikelets than other spike elements.

Table 3. Results of evaluation of dominance in F₁

Hybrid ♀	1973				1974			
	S290		M 553d		S290		M 553d	
	dominance							
	[25]	[26]	[25]	[26]	[25]	[26]	[25]	[26]
Ac	0.71 **	79.5	0.74 **	69.6	1.17 ***	103.7	2.87 ***	118.6
IBO	-0.62 *	16.8	1.36 ***	>200.0	0.52 **	96.9	2.00 ***	>200.0
Gt	0.28	63.1	2.18 ***	>200.0	0.09	52.6	0.80 ***	103.3
P62	-1.95 ***	6.7	0.30	59.8	-1.01 ***	25.5	1.27 ***	109.8
Dw	-3.36 ***	15.8	0.20	55.4	-2.87 ***	78.9	1.71 ***	>200.0

* P<0.05.
 ** P<0.01.
 *** P<0.001.

In addition to degree of expression of the character in cultivars and hybrids, the nature of inheritance thereof under different vegetation conditions is also important. Table 3 lists the results of evaluation of dominance, calculated by two methods. The estimates made according to [25] make it possible to determine the reliability of deviation of mean value

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for the F_1 hybrid from the parent mean, while calculations according to [26] permit expression of the degree of dominance as a percentage. As we see, in 16 out of 20 cases, the mean value for F_1 differs reliably from the mean for the original parents, and in 5 cases the deviation has a minus sign. Intermediate inheritance was manifested in 3 hybrids in 1973 ($Gt \times S29$, $P62 \times M553$, $Dw \times M553$) and 1 in 1973 ($Gt \times S29$). Incomplete dominance in the direction of the parent with the greater number of spikelets per spike was observed in two hybrids ($Ac \times S29$ in 1973 and $IBO \times S29$ in 1974). Complete dominance in the direction of the parent with the greater number of spikelets was manifested in 3 hybrids in 1974 ($Ac \times S29$, $Gt \times M553$, $P62 \times M553$). In the case of using tester M553, overdominance was expressed in 2 hybrids in 1973 ($IBO \times M553$, $Gt \times M553$) and 3 in 1974 ($Ac \times M553$, $IBO \times M553$, $Dw \times M553$).

There was partial dominance in the direction of the parent with fewer spikelets in two hybrid combinations ($IBO \times S29$ and $P62 \times S29$). The estimates with a negative sign for hybrid $Dw \times S29$ are indicative of inhibition, rather than dominance, since the number of spikelets was reliably lower in the heterozygote than the parent with lower number of spikelets per spike.

The obtained estimates thus indicate that the nature of inheritance of the character changes significantly as a function of environmental conditions. It was demonstrated that both maternal and paternal (tester) plants differ appreciably from one another in genetic system of control of the character under study. While there was mainly expression of intermediate inheritance, partial dominance, in hybrids derived from tester S29, and in 3 of these cases in the direction of the parent with fewer spikelets, in hybrids derived from tester M553 we observed complete dominance and overdominance, along with intermediate inheritance.

In order to predict the results of selection in early segregant generations, we must have information about manifestation of the heterosis effect in heterozygotes, since the less heterosis is expressed, the earlier the generations (F_2 , F_3) when one can start selection in the segregating population [27].

Analysis of the data in Table 4 shows that heterosis is expressed in a small part of the hybrids according to number of spikelets per spike. A reliable heterosis effect was not demonstrable in any of the hybrids involving tester S29. As a rule, the F_1 hybrids are reliably inferior to the best parent according to number of spikelets per spike. With participation of tester M553, heterosis was expressed in hybrids $IBO \times M553$ (6.5%), $Gt \times M553$ (10.3%) in 1973, $Ac \times M553$ (4.5%), $IBO \times M553$ (9.6%) and $Dw \times M553$ (9.7%) in 1974.

The results obtained on expression of heterosis are consistent with the estimates of dominance in F_1 (see Table 3). A reliable heterosis effect was manifested in hybrids, for which the estimates revealed overdominance. It must be noted that our analysis did not enable us to determine which genetic systems were responsible for expression of heterosis. The

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attenuation of the character in F_2 , as compared to F_1 , in 1973 can be attributed to the fact that heterosis is determined by heterozygosity of loci controlling the number of spikelets per spike. But this interpretation cannot apply to the results obtained in 1974, when heterosis persisted in F_2 at the same level as in F_1 . Evidently, the heterosis effect in hybrids is related not only to heterozygosity, but other types of gene action and interaction, as well as genotype \times environment interaction.

Table 4. Deviation of F_1 and F_2 hybrids from parent with greater number of spikelets per spike (d)*

Hyb- rid	1973								1974							
	S 29d				M 553d				S 29d				M 553d			
	F_1		F_2		F_1		F_2		F_1		F_2		F_1		F_2	
	d	%	d	%	d	%	d	%	d	%	d	%	d	%	d	%
Ac	-0.49	3.2	-0.92 **	5.3	-1.15 ***	6.8	-0.01	0.2	0.08	0.5	-0.30	2.0	0.78 ***	4.5	1.01 ***	5.9
IBO	-1.54 ***	8.9	-1.12 ***	6.5	1.13 ***	6.5	-0.12	0.7	-0.04	0.2	0.00	0.0	1.65 ***	9.6	1.37 ***	8.0
Gt	-0.79 *	4.5	0.29	1.6	1.81 ***	10.3	0.96 ***	5.5	-1.67 ***	8.9	-2.13 ***	11.4	0.05	0.3	-0.85 ***	4.6
P 82	-4.20 ***	21.1	-4.03 ***	20.2	-1.25 ***	6.3	-1.13 ***	5.7	-3.09 ***	16.0	-2.74 ***	14.2	0.21	1.1	-1.18 ***	6.1
Dw	-5.92 ***	28.8	-5.87 ***	28.6	-1.68 ***	8.1	-1.12 ***	5.4	-3.74 ***	21.7	-3.04 ***	17.6	1.67 ***	9.7	1.67 ***	9.7

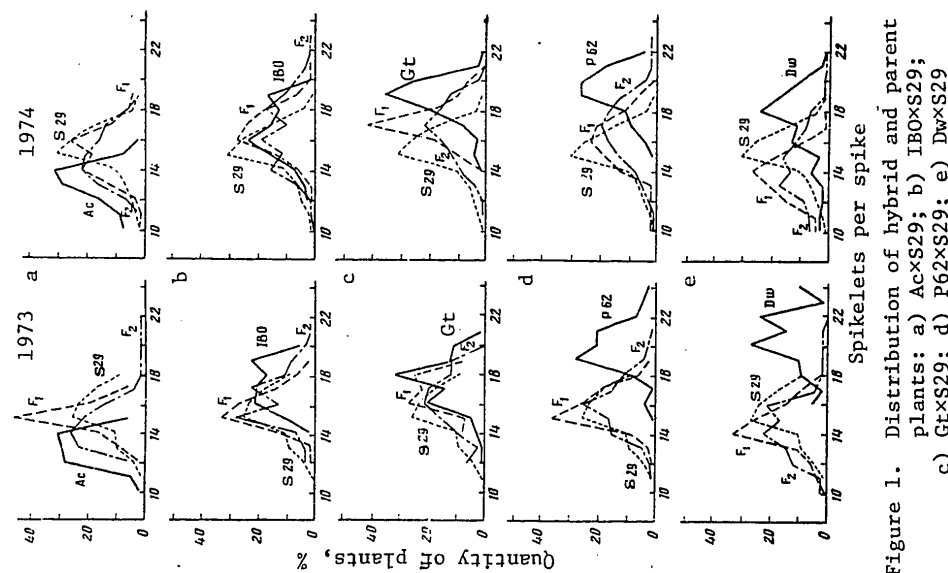
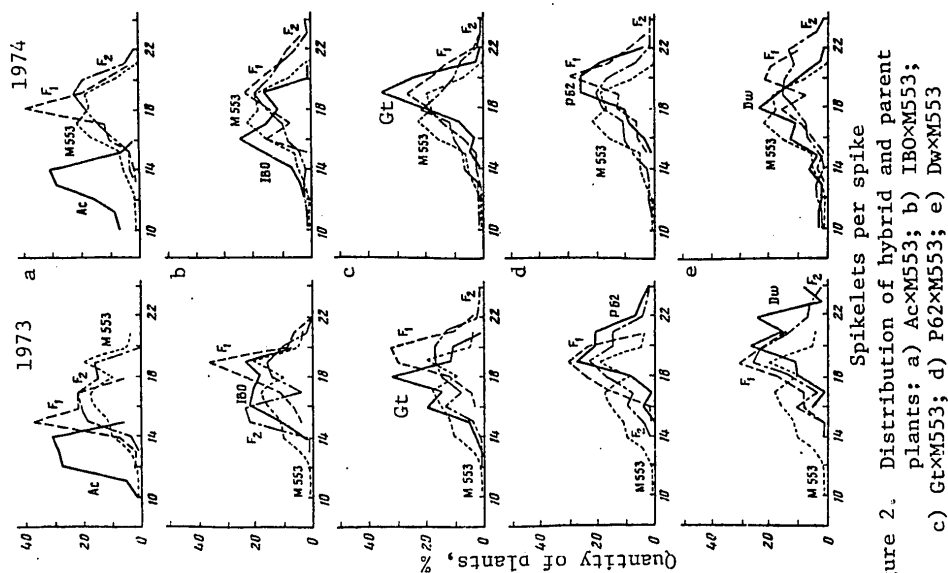
*See footnote to Table 3.

Table 5. Variances (σ^2) and indices of heritability (H_b)

Hyb- rid cul- tiv.	1973								1974							
	σ^2				H_b				σ^2				H_b			
	P		S 29d		M 553d		H_b		P		S 29d		M 553d		H_b	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Ac	1.16	1.23	3.31	0.53	1.47	2.38	0.02	1.98	2.79	2.93	0.07	2.21	3.46	0.23	0.23	0.23
IBO	2.37	1.72	3.72	0.44	2.11	3.66	0.19	3.81	2.61	5.18	0.40	3.97	5.67	0.29	0.29	0.29
Gt	2.68	1.93	3.77	0.40	1.78	5.42	0.47	2.06	1.43	6.10	0.68	4.44	5.38	0.30	0.30	0.30
P 82	3.04	1.73	3.38	0.36	1.21	4.10	0.35	2.34	2.90	4.31	0.33	4.04	4.50	0.18	0.18	0.18
Dw	3.85	2.04	4.79	0.45	2.32	4.22	0.19	6.82	2.57	8.37	0.53	6.00	7.30	0.22	0.22	0.22
S 29	2.57	-	-	-	-	-	-	3.36	-	-	-	-	-	-	-	-
M 553	5.20	-	-	-	-	-	-	4.28	-	-	-	-	-	-	-	-

Since overdominance in most hybrids makes a negligible contribution to phenotypic variability of the character in F_2 , it is possible to calculate the indices of heritability in the general sense by the formula used previously [28]. Table 5 lists the variances for parents and hybrids, as well as indices of heritability. As we see, the variances reflecting general phenotypic variability of the character fluctuate markedly, depending on the genotype and vegetation conditions. In parent cultivars, variance ranged from 1.16 to 5.20 in 1973 and from 1.98 to 6.62 in 1974. In hybrids involving tester S29, variances ranged from 1.23 to 2.04 in F_1 and from 3.31 to 4.79 in F_2 , in 1973; the figures for 1974 were 1.43 to 2.90 and 2.93 to 8.39, respectively. In hybrids involving tester M553, the variances ranged from 1.21 to 2.32 in F_1 and from 2.38 to 5.42 in F_2 , in 1973; in 1974, the figures were 2.21 to 6.00 and 3.46 to 7.30, respectively.

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The variance was higher in all F_2 hybrids than in F_1 , which is indicative of segregation of genes controlling the number of spikelets per spike. However, we were impressed by cultivars M553 and Dw: the variances were higher in the former in 1973 and in the latter in 1973 than in F_2 hybrids. The high values of variances cannot be attributed to heterogeneity of the cultivars for this character, since studies thereof prior to use in the experiment revealed that both cultivars are rather homogeneous genotypically with respect to number of spikelets per spike. At the same time, we found that M553 was heterogeneous in rate of plant development between germination and heading, while foreign cultivar Dw was extremely sensitive to local conditions. Under adverse vegetation conditions (shortage of water) in 1974, there was a sharp reduction in germination--heading period in cultivar Dw.

On the basis of these data, it is assumed that the high phenotypic variability of spikelets per spike in M553 is related to heterogeneity of the plants with respect to heading date and in Dw, to plant sensitivity at this stage to environmental conditions. This hypothesis is confirmed by the fact that there is a close correlation in ontogenesis between the rate of development and formation of primordium of different spike elements. However, in view of the fact that the variance is considerably lower in most hybrids in F_1 than in F_2 , there is a possibility of determining the index of heritability. It is also important that the variance is lower in all parent components, with the exception of M553 and Dw, than in F_2 hybrids.

The indices of heritability (see Table 5) in hybrids involving tester S29 ranged from 0.36 to 0.53 in 1973 and from 0.07 to 0.66 in 1974, whereas in hybrids involving tester M553 they ranged from 0.02 to 0.47 and 0.18 to 0.30, respectively. These results indicate that the variability of the character, with regard to relative phenotypic expression in parents and hybrids, under different vegetation conditions led to significant fluctuation of indices of heritability.

Probably, the heritability indices alone are not enough to predict selection in segregating generations. The curves of plant distribution according to number of spikelets per spike in parents, F_1 and F_2 hybrids provide the most reliable information (Figures 1 and 2). On the whole, it should be noted that the distribution of the plants was close to normal, both for parents and hybrids, although some deviation from normal was observed for some cultivars and hybrids. A double-peaked curve of plant distribution was demonstrated for cultivars Gt and Dw (1973), IBO (1974), M553 (1973), in F_1 Ac×S29 (1974) and Dw×M553 (1974) hybrids. However, these deviations are not related to genotypic differences between plants, but to genotype sensitivity to environmental conditions and their reaction to different environmental factors at different ontogenetic stages.

There was expression of positive transgressive segregation in some F_2 hybrids, although it was unstable in different years. In essence,

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transgression was expressed in hybrids involving tester M553. In 1974, transgression was observed in all hybrids involving this tester and in 1973, in only one hybrid, Gt×M553. In the hybrids involving tester S29, positive transgression was expressed in 2 cases in 1973 (Ac×S29, IBO×S29) and 2 others in 1974 (IBO×S29, P62×S29).

The nature of segregation in F₂ indicates that the character under study is controlled by a large number of genes with additive action, which express varying degrees of dominance and overdominance, depending on environmental conditions. Analysis of the results referable to testers shows that Siberian cultivar M553 is the more valuable source of genes than cultivar S29 for breeding to augment the number of spikelets per spike, since hybrids involving M553 form more spikelets per spike. Of the foreign cultivars, which are less adapted to Siberian conditions, short-stemmed cultivars D2 and P62, and long-stemmed Gt are of the greatest value. On the basis of the data on transgression, it is expected that by means of selection in early segregating generations of hybrid combinations P62×M553, Dw×M553 and Gt×M553 we can isolate lines with more spikelets per spike than the best original cultivars. The only question is whether there will be stable expression of this trait under different vegetation conditions.

The author wishes to express his sincere appreciation to S. A. Sadykova, K. Ye. Shnayder, L. K. Getman and Ye. Ya. Reger for their technical assistance with the experiment.

Conclusions

Genetic analysis revealed that the cultivars studied differ substantially in nature of manifestation and genetic control of the character, and reaction to vegetation conditions.

In F₁ of hybrids derived from tester S29, there was expression of intermediate inheritance, partial and incomplete dominance, and in three cases this was in the direction of the parent with the smaller number of spikelets per spike.

In F₁ of hybrids derived from tester M553, there was expression of intermediate inheritance, complete dominance and overdominance.

The estimates obtained are indicative of unstable level and direction of dominance, and expression of the heterosis effect when the material is grown under different conditions.

On the basis of genetic analysis, it is assumed that cultivars Gt, P62, Dw and M553 may serve as sources of genes to augment the number of spikelets per spike in breeding practice.

There are 5 tables and 2 illustrations; bibliography lists 28 items.

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BIBLIOGRAPHY

1. Filipchenko, Yu. A. "Genetics of Soft Wheat," Moscow--Leningrad, OGIZ [Association of State Publishing Houses], 1934, p 262.
2. Borojevic, S. "Type of Inheritance and Heritability of Quantitative Traits in Hybrids of Different Wheat Cultivars," SAVREMENA POLJOPR. [Modern Agriculture (Croatian)], Vol 13, No 7-8, 1965, 587.
3. Mirzinski, J., and Jankovich, M. "Manifestation of Heterosis in Some Wheat Hybrids," Ibid, Vol 14, No 3, 1966, 247.
4. Rusanovschi, G. "Contribution to the Study of Heterosis in Wheat," "An. Inst. cercetari cereale si plante tehn. Fundulea [Fundulea Research Institute for Cereals and Technical Crops (Rumanian)], Vol 34, 1967, 29.
5. Sanhu, T. S., and Singh, G. "Studies on Expression of Heterosis in Wheat," INDIAN J. AGRIC. SCI., Vol 37, No 6, 1967, 544.
6. Mihaljev, I. "Investigation of Heritability of Quantitative Properties Related to Yield of Certain Wheat Cultivars," SAVEREMNA POLJOPR., Vol 16, No 1, 1968, 47.
7. Jankovic, M. "Inheritance of Stem Length and Number of Kernels in Wheat Spike," Ibid, Vol 17, No 7-8, 1969, 781.
8. Singh, K. B.; Sharma, D.; Mehndiratta, P. D. "Study of Combining Ability and Genetic Parameters for Yield and Its Components in Wheat," JAP. J. GENET., Vol 44, No 36, 1969, 367.
9. Mamonov, L. K. "Influence of Genotype and Environmental Conditions on Some Indices of Yield Structure in Spring Wheat," GENETIKA [Genetics], Vol 6, No 9, 1970, 23.
10. Akhmedov, E. G. "Inheritance of Quantitative Characters in Ecologically Remote First Generation Hybrids in Karabakh," "Tr. in-ta genet. i selektsii AN AzSSR" [Works of the Institute of Genetics and Breeding, Azerbaijan Academy of Sciences], No 6, 1970, 118.
11. Chapman, S. R., and McNeal, F. H. "Gene Action for Yield Components and Plant Height in a Spring Wheat Cross," CROP SCI., Vol 11, No 3, 1971, 384.
12. Jain, R. P., and Aulakh, H. S. "Variability in Wheat (Triticum aestivum L.)," INDIAN J. AGRIC. SCI., Vol 41, No 4, 1971, 297.
13. Tapu, Z. "Estimation of Genetic Components of Heterosis and Transgressive Inheritance of Productivity of Wheat Spike," "An. Inst. cerc. cereale plante tehn., Fundulea, Vol 38, 1970, 19.

FOR OFFICIAL USE ONLY

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14. Schmalz, H. "Study of Inheritance of Number of Spikelets per Spike in Spring Wheat [*Triticum aestivum* (L.) Thell. ssp. vulgare (Vill.) MK]," ARCH. ZUCHTUNGSFORSCH., Vol 2, No 2, 1972, 153.
15. Rajinder, K.; Anand, S. C.; and Virk, D. S. "Heritability and Genetic Advance of Some Quantitative Characters in Crosses of Wheat (*Triticum aestivum* L.)," J. RES., Vol 9, No 4, 1972, 515.
16. Khadr, F. H.; Ismail, A. M.; and Morsy, M. S. "Heritabilities of Quantitative Traits Estimated by Different Methods in Generations of Wheat Crosses," EGYPT. J. GENET. AND CYTOL., Vol 1, No 2, 1972, 263.
17. Hassanien, E. H.; Ibrahim, H. A.; Selim, A. I. A.; and Attia, S. E. A. "Heterosis and Combining Ability in a Spring Wheat Diallele Cross (Grain Yield and Its Components)," SAVREMENA POLJOPR., Vol 21, No 7-8, 1973, 33.
18. Lubnin, A. N. "Heterosis and Inheritance of Principal Breeding Characters in F₁ of Some Winter Wheat Cultivar Crosses," Byul. Vses. n.-i. in-ta rasteniyevodstva imeni N. I. Vavilova" [Bulletin of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov], Vyp 32, 1973, 10.
19. Hsu, P., and Walton, P. D. "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54.
20. Idem, "The Quantitative Inheritance in Spring Wheat of Morphological Structures Above the Flag Leaf Node," CANAD. J. GENET. AND CYTOL., Vol 12, No 4, 1970, 738.
21. Walton, P. D. "The Use of Factor Analysis in Determining Characters for Yield Selection in Wheat," EUPHYTICA, Vol 20, No 3, 1971, 416.
22. Idem, "Quantitative Inheritance of Yield and Associated Factors in Spring Wheat," Ibid, Vol 21, No 3, 1972, 553.
23. Tsil'ke, R. A. "Variability of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1974, 31.
24. Idem, "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 1: Stem Length," GENETIKA, Vol 11, No 2, 1975, 14.
25. Fontdevila, A. "Genotype-Temperature Interaction in *Drosophila Melanogaster*. II. Body Weight," GENETICS, Vol 73, No 1, 1973, 125.

FOR OFFICIAL USE ONLY

26. Gustaffson, A., and Dormling, I. "Dominance and Overdominance in Phytotron Analysis of Monohybrid Barley," HEREDITAS, Vol 70, No 2, 1972, 185.
27. Briggs, F., and Knowles, P. "Scientific Bases of Plant Breeding," Moscow, Kolos, 1972, p 339.
28. Purdy, J. L., and Crane, P. L. "Inheritance of Drying Rate in 'Mature' Corn (Zea mays L.)," CROP SCI., Vol 7, No 4, 1967, 294. [485-10,657]

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STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 5: NUMBER OF KERNELS PER SPIKE

Moscow GENETIKA in Russian Vol 13, No 11, 1977 pp 1889-1899

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of
Agriculture, Omsk, submitted 7 Sep 76]

[Text] Introduction

Wheat yield is made up of two elements, number of productive spikes per unit area and weight of kernels. Each of these elements is controlled by a complex genetic system that interacts closely with environmental conditions. Kernel weight is related to kernel size and number of kernels per head. The worldwide pool of genes of soft wheat is characterized by significant diversity of head productivity. Varietal differences in this integral character are attributable to the direction of selection and environmental conditions, under which a variety is being developed. No matter what set of factors characterize the conditions of any geographic region, the breeder always tries to develop a variety with maximum expression of this character. It is assumed that the genetic potential of wheat has not yet been expressed in modern cultivars, with respect to number of grains per spike. And it should be noted that the genetic system of control of morphogenesis of this character is very sensitive to various environmental factors; for this reason the intensity of expression thereof fluctuates markedly, depending on vegetation conditions. The phenotypic lability of the character creates difficulties when selecting and evaluating breeding material, especially at the early stages of selection.

Studies have shown that this trait is usually characterized by polygenic inheritance. Analysis of diallelic F_1 hybrids established that most of the genotypic variability is attributable to genes with additive action, while in some cultivars the number of kernels per spike is controlled by genes with a dominant effect [1]. In another study [2], it is indicated that this character is controlled mainly by genes with additive action. Some researchers [3-6] obtained high heritability indices. However, there is information to the effect that this trait is characterized by low heritability [7]. In some studies it was shown that the heterosis effect

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is expressed in F₁ [8, 10], and in others [11, 12] that none is manifested. Transgressive segregation in F₂ was observed in many winter wheat hybrids [13]. Studies of an F₁ hybrid raised under different vegetation conditions revealed that overdominance was expressed under some conditions and total dominance of the parent with the greater number of kernels per spike in others; in the former case, the coefficient of heritability constituted 0.18 and in the latter 0.49 [14].

The contradictory conclusions of researchers are related to variability of the nature of inheritance of this character under the influence of the environment and genotypic diversity of the material used in the crosses.

Few studies have been pursued in Siberia of inheritance of quantitative characters that are important for breeding programs to develop new and highly productive wheat cultivars [5, 14]. In this article, we report the results of an experimental study of inheritance of number of kernels per spike in soft winter wheat topcrosses.

Material and Methods

We used as maternal plants five cultivars obtained from the collection of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov: Dwarf S₆₉₆ A-7 (Dw), IBO-3048-433 (IBO), Pitic 62 (P62), Acadia (Ac) and Gun To-may (Gt). Saratovskaya 29 (S29) and Mil'turun 553 (M553), which are cultivars widely grown in Siberia, served as paternal parents (testers). The material was matched in accordance with the specifications for a modern cultivar. Each cultivar used in the experiment was characterized by some unique, economically valuable character or set of characters. The Dw dwarf, unlike most short-stemmed cultivars, forms a large and multispiket head, and it is resistant to brown rust; IBO is exceptionally resistant to lodging, it is not stricken by powdery mildew and has a multiflorescent spikelet; P62 is a cultivar of the intensive type that is very responsive to high soil fertility, with a productive spike; Ac is drought resistant and has a high grade kernel; Gt is a variety with productive head and large kernels; S29 has an excellent kernel quality and high homeostasis; M553 is well adapted to local conditions, which is attributable to embryonic plasma that has undergone a prolonged natural and artificial evolutionary process (selection) in the steppe regions of West Siberia. Before being used in the crosses, the above cultivars were studied for 3-5 years in the genetic collection of the laboratory. Additional information about the base material and experimental methods is furnished in our first report [15].

Experimental Section and Discussion

The results of variance analysis listed in Table 1 indicate that differences are significant, not only between variants (parents and hybrids), but between replications (blocks). In 1974, the mean square (ms) was more than 2 times greater for the variants, almost 5 times greater for the replications

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and almost 2 times greater for random deviations than in 1973. Only the mean square of variant \times block interaction in 1974 was smaller than in 1973. Thus, under the less favorable vegetation conditions (1974) there was intensification of differences between both variants and blocks. Variance analysis clearly shows that this character is very sensitive to environmental conditions. Heterogeneity of the experimental plot, with regard to water supply and nutrition enhanced drastically the phenotypic variability of the character.

Table 1. Results of variance analysis

Sources of variability	1973			1974		
	df	ms	F	df	ms	F
Variant, A	26	2168,04	60,34 **	26	4592,34	77,00 **
Replication, B	3	431,30	13,19 **	3	2203,54	36,95 **
AxB interaction	78	221,02	0,76 **	78	94,38	1,58 *
Random deviations	26	32,49	—	5077	59,04	—

* $P < 0,01$; ** $P < 0,001$.Table 2. Number of kernels per spike in parents and hybrids ($\bar{x} \pm s_x$)

Cultivar, hybrid	P	S 29		M 553	
		F ₁	F ₂	F ₁	F ₂
1973					
Ac	22,25 \pm 0,32	27,28 \pm 0,32	37,22 \pm 0,03	23,89 \pm 0,36	25,71 \pm 0,81
Dw	34,12 \pm 0,82	33,52 \pm 0,15	32,49 \pm 0,72	37,96 \pm 0,59	37,80 \pm 0,91
Gt	36,06 \pm 0,95	29,45 \pm 0,30	30,04 \pm 0,53	37,50 \pm 0,59	32,88 \pm 0,92
IBO	38,04 \pm 0,79	30,40 \pm 0,48	30,75 \pm 0,03	34,90 \pm 0,66	32,79 \pm 0,87
P 62	42,84 \pm 1,09	36,12 \pm 0,66	34,55 \pm 0,72	39,05 \pm 0,40	37,69 \pm 0,90
S29	31,32 \pm 0,49	—	—	—	—
M 553	27,08 \pm 0,73	—	—	—	—
\bar{x}_0	33,19	30,03	31,13	34,66	33,37
1974					
Ac	20,96 \pm 0,39	26,40 \pm 0,50	25,50 \pm 0,35	23,52 \pm 0,45	24,51 \pm 0,33
Dw	20,83 \pm 0,01	31,58 \pm 0,62	29,17 \pm 0,36	34,40 \pm 0,73	33,84 \pm 0,45
Gt	30,04 \pm 0,59	30,45 \pm 0,47	29,06 \pm 0,38	34,74 \pm 0,73	31,04 \pm 0,03
IBO	39,55 \pm 0,84	30,46 \pm 0,06	28,98 \pm 0,48	38,54 \pm 1,07	35,30 \pm 0,58
P 62	36,02 \pm 1,03	36,06 \pm 0,50	33,70 \pm 0,40	37,08 \pm 0,87	37,28 \pm 0,52
S29	29,30 \pm 0,51	—	—	—	—
M 553	31,20 \pm 0,78	—	—	—	—
\bar{x}_0	30,19	30,93	29,29	33,66	32,57

Table 2 lists data on number of kernels per head in parents and hybrids. The foreign cultivars used as maternal plants differ appreciably in number of kernels per spike. In these cultivars, the number of kernels ranged from 22.25 (Ac) to 42.84 (P62) in 1973 and from 20.83 (Dw) to 39.55 (IBO) in 1974. There was also a reliable difference between cultivars S29 and M553, used as paternal parents (testers), which are raised extensively locally: the difference between them constituted 4.24 kernels in 1973 and 4.96 in 1974. Typically enough, a greater number of kernels per spike was formed in S29 in 1973, whereas in 1974, which was a less favorable year with regard to water, this applied to M553. This is indicative of marked interaction between the genotype and environment. The group means

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(\bar{x}_0) contain valuable information; they indicate that tester M553, which formed fewer kernels per spike in 1973 than tester S29, produced hybrids with a greater number of kernels per spike. Consequently, with regard to this trait, M553 is characterized by greater overall combining ability than cultivar S29.

It should also be noted that the nonlocal cultivars differ markedly in reaction to vegetation conditions. Thus, early ripening cultivar Ac formed 22.25 kernels per spike and late ripening Dw formed 34.12 kernels in 1973, whereas these cultivars virtually failed to differ in 1974, forming 20.96 and 20.83 kernels per spike, respectively.

Expression of genotype \times environment interaction was not as marked in hybrids as in cultivars. In 1973, in hybrids involving tester S29, the number of kernels ranged from 26.46 (IBO \times S29) to 36.42 (P62 \times S29) in F₁ and from 27.22 (Ac \times S29) to 34.55 (P62 \times S29) in F₂; for hybrids involving tester M553, the number of kernels ranged from 23.89 (Ac \times M553) to 39.05 (P62 \times M553) in F₁ and from 25.71 (Ac \times M553) to 37.80 (Dw \times M553) in F₂. In 1974, the number of kernels in hybrids involving tester S29 ranged from 26.10 (Ac \times S29) to 36.06 (P62 \times S29) in F₁ and from 25.50 (Ac \times S29) to 33.76 (P62 \times S29) in F₂, whereas for hybrids involving tester M553, the figures were 23.52 (Ac \times M553) to 38.54 (IBO \times M553) in F₁ and 24.51 (Ac \times M553) to 37.28 (P62 \times M553) in F₂.

Analysis of group means (\bar{x}_0) of different generations showed that, on the whole, F₂ was slightly inferior to F₁ in number of kernels per spike, although significant differences between hybrids were observed for this index. This shows that genes with additive action make the main contribution to the system of genetic control of the character but, at the same time, some hybrids present dominance. Table 3 lists the estimates of dominance made by two methods [16, 17].

Table 3. Results of estimating dominance in F₁

Hybrid	1973				1974			
	S 29		M 553		S 29		M 553	
	numb. kern.	%	numb. kern.	%	numb. kern.	%	numb. kern.	%
Ac	0,50	55,5	-0,77	33,0	0,97	61,6	-4,09 ***	19,2
Dw	0,80	78,6	7,36 ***	154,5	6,52 ***	126,9	6,80 ***	101,0
Gt	-4,34 ***	39,4	5,93 ***	116,0	-2,22 **	17,1	-0,41	27,0
IBO	-8,52 ***	66,4	2,04 *	67,8	-3,96 ***	11,3	1,64 *	86,9
P 62	-0,06	44,3	4,09 ***	76,0	3,40 ***	100,6	1,94 *	160,2

* $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

In 14 out of 20 cases, the mean value of the character in the F₁ hybrid deviated reliably from the mean between parents, the deviation being negative in 5 cases, which is indicative either of inhibition or dominance of the parent with fewer kernels per spike. In 1973, 4 hybrids (Ac \times S29,

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Dw×S29, P62×S29, Ac×M553) expressed intermediate inheritance, 2 (Dw×M553, Gt×M553) overdominance, 1 (IBO×M553) partial dominance and 1 (P62×M553) incomplete dominance of the parent with the greater number of kernels per spike, and in 2 hybrids (Gt×S29, IBO×S29) there was inhibition, i.e., F₁ was reliably inferior to the parent with less expression of the character. It is assumed that inhibition is related to the epistatic action of genes, since more kernels per spike were formed in F₂ of these hybrids than in F₁. We should also call attention to the fact that this type of gene action is modified by environmental conditions. No inhibition was manifested in F₁ in 1974.

In 1974, there was expression of intermediate inheritance in 2 hybrids (Ac×S29, Gt×M553), overdominance in 2 (Dw×S29, P62×M553), complete dominance in 2 (P62×S29, Dw×M553), incomplete dominance of the parent with more kernels per spike in 1 (IBO×M553) and incomplete dominance of the parent with fewer kernels in 3 hybrids (Gt×S29, IBO×S29, Ac×M553).

Such lability of inheritance is related mainly to the fact that the F₁ hybrids and particularly the parent cultivars are strongly dependent on vegetation conditions (genotype × year interaction). The same nature of inheritance (intermediate) under different vegetation conditions was expressed only in hybrid Ac×S29. The data in Table 4 are indicative of the lability of nature of inheritance. There was expression of reliable heterosis in F₁ of one hybrid in 1973 (Dw×M553) and one in 1974 (Dw×S29); the figures were 11.2% in the former case and 7.8% in the latter. F₁ did not differ reliably from the best parent for 2 hybrids in 1973 (Dw×S29, Gt×M553) and 5 in 1974 (P62×S29, Dw×M553, Gt×M553, P62×M553, IBO×M553). In all other combinations, F₁ was reliably inferior to the best parent with respect to kernels per spike. F₂ was reliably inferior to F₁ in 4 hybrids in 1973 (IBO×S29, Gt×M553, Ac×M553, IBO×M553) and 3 in 1974 (P62×S29, Gt×M553, IBO×M553).

Table 4. Deviation of F₁ and F₂ hybrids from best parent (d)

Hybrid	S29				M553			
	P ₁		P ₂		P ₁		P ₂	
	d	%	d	%	d	%	d	%
1973								
Ac	-4.04 **	12.9	-4.10 **	13.1	-3.19 **	11.8	-1.37	5.1
Dw	-0.60	1.8	-1.63	4.8	3.84 **	11.2	3.68 **	10.8
Gt	-6.61 **	18.3	-5.42 **	15.0	1.44	4.0	-3.18 **	8.5
IBO	-12.18 **	31.5	-7.89 **	20.4	-3.74 **	9.7	-5.85 **	15.1
P62	-6.42 **	15.0	-6.29 **	14.7	-3.70 **	8.8	-5.15 **	12.0
1974								
Ac	-3.20 **	10.9	-3.80 **	13.0	-10.74 **	31.3	-8.75 **	28.4
Dw	2.28 **	7.8	-0.13	0.4	0.14	0.4	-0.42	1.2
Gt	-5.59 **	15.5	-6.98 **	19.4	-1.30	3.8	-4.10 **	11.4
IBO	-9.09 **	23.0	-10.57 **	28.7	-1.01	2.6	-4.75 **	10.7
P62	0.04	0.1	-2.26 *	6.3	1.06	2.9	1.46	3.5

* P<0.01; ** P<0.001.

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Table 5. Variances (σ^2) in parents, F₁ and F₂ hybrids

Таблица 5

Значение дисперсии (σ^2) у родителей и гибридов F₁ и F₂

Cultiv., hybrid	1973						1974					
	P			S29			P			S29		
	F ₁	F ₂	M553	F ₁	F ₂	M553	F ₁	F ₂	M553	F ₁	F ₂	M553
Ac	7.96	8.25	32.02	10.43	52.03	19.25	32.87	34.05	24.55	34.20		
Dw	51.39	34.15	42.05	27.86	65.88	45.84	40.97	44.74	56.89	64.68		
Gt	72.72	11.97	22.36	28.25	68.46	40.29	26.14	47.58	63.69	131.02		
IBO	50.23	18.18	69.84	31.80	59.91	89.53	54.16	69.59	72.88	101.93		
P62	94.97	31.83	41.81	12.74	65.51	101.78	47.57	51.69	85.20	93.88		
S29	19.36	--	--	--	--	34.29	--	--	--	--		
M553	42.71	--	--	--	--	76.03	--	--	--	--		

Table 5 lists the variances (σ^2) for parents, F₁ and F₂ hybrids, which are indicative of great lability of the character, and the original cultivars differ markedly in this index. We were impressed by the fact that not only the foreign cultivars, but the one bred locally (M553), are characterized by high intrapopulation phenotypic variability. The values of variances fluctuate very markedly, depending on plant vegetation conditions. In all cultivars, with the exception of Dw and Gt, variance was higher in 1974 than 1973. In 1973, variance fluctuated from 7.96 in Ac to 94.97 in P62, whereas in 1974 it ranged from 19.25 to 104.78. In 1973, the hybrids derived from tester S29 showed variances ranging from 8.25 (Ac×S29) to 34.83 (P62×S29) in F₁ and from 22.36 (Gt×S29) to 69.84 (IBO×S29) in F₂; in hybrids involving tester M553, the figures were 10.43 (Ac×M553) to 34.80 (IBO×M553) in F₁ and 52.03 (Ac×M553) to 68.46 (Gt×M553) in F₂. In 1974, the variance of hybrids involving tester S29 ranged from 32.80 (Ac×S29) to 54.16 (IBO×S29) in F₁ and from 34.05 (Ac×S29) to 69.50 (IBO×S29) in F₂, and for hybrids involving tester M553 the figures were 24.55 (Ac×M553) to 85.20 (P62×M553) in F₁ and 34.20 (Ac×M553) to 131.02 (Gt×M553) in F₂. Of course, with such high values for the variances of parents, there is no purpose to calculation of coefficients of heritability, since this index would be negative for a number of hybrid combinations.

Before we discuss the causes of such high variances, we should analyze the results of distribution of parent and hybrid plants according to number of kernels per spike (Tables 6 and 7). On the whole, the distribution is close to normal for parents, as well as F₁ and F₂ hybrids. Normal distribution was particularly distinct in 1974, when more plants were analyzed than in 1973. In 1973, the size of the samples constituted 80 for cultivars, F₁ and F₂ hybrids and in 1974 the samples constituted 120 plants for cultivars and F₁ hybrids, and 300 plants for F₂. As we see, the amplitude of variability of the character fluctuates over a wide range. In 1973, the number of classes within which the set of variable values were contained ranged from 7 (Ac) to 17 (P62) for parents, 5 (Ac×S29) to 11 (Dw×S29, P62×S29) for hybrids involving tester S29 in F₁ and 7 (Gt×S29) to 19 (IBO×S29) in F₂; for hybrids involving tester M553, the range was from 8 (Ac×M553, Dw×M553) to 14 (IBO×M553) in F₁ and 13 (P62×M553) to 16 (Gt×M553) in F₂. In 1974, this index ranged from 11 (Ac) to 17 (P62) in parents, 10 (Gt×S29) to 16 (Dw×S29) in F₁ hybrids derived from S29, 13 (Ac×S29) to 19 (IBO×S29) in F₂ of these hybrids, and for those derived from tester M553, 11 (Ac×M553) to 18 (P62×M553) in F₁ and 14 (Ac×M553) to 22 (P62×M553) in F₂.

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Table 6. Distribution of parent, F₁ and F₂ plants in 1973 according to kernels per spike (%)

Class	Dw		Ac		Gt		Dw		Ac		Gt		Dw		Ac		Gt		Dw		Ac		Gt	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
7-9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10-12	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13-15	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16-18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19-21	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22-24	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
25-27	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
28-30	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
31-33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34-36	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
37-39	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
40-42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
43-45	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
46-48	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
49-51	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
52-54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
55-57	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
58-60	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
61-63	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
64-66	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
67-69	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
70-72	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
73-75	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Note: Here and in Table 7, boldface vertical lines refer to maternal classes and dotted lines to paternal classes

Table 7. Distribution of parent, F₁ and F₂ plants in 1974 according to kernels per spike (%)

Class	Dw		Ac		Gt		Dw		Ac		Gt		Dw		Ac		Gt		Dw		Ac		Gt	
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂
1-3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4-6	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7-9	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10-12	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13-15	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16-18	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19-21	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22-24	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
25-27	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
28-30	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
31-33	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
34-36	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
37-39	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
40-42	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
43-45	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
46-48	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
49-51	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
52-54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
55-57	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
58-60	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
61-63	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
64-66	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
67-69	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
70-72	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
73-75	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

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Analysis of the sets of variables shows that not only F_2 , but most cultivars and F_1 hybrids are characterized by high phenotypic variability. While variability in F_2 is attributable, on the one hand, to segregation of genes that control the character and, on the other hand, to environmental conditions, it is difficult to explain the high variability of the trait in homozygous parents and genotypically homogeneous F_1 hybrids. Only the early ripening Canadian cultivar Ac and average ripening locally raised S29 are characterized by low variability. Under the less clement conditions of 1974, variability of the trait was high in most cultivars and hybrids. The variances were particularly high for average ripening foreign cultivars IBO and P62, as well as late ripening Siberian cultivar M553. It is assumed that the degree of phenotypic variability is related to three causes.

The first is sensitivity of the genotype to environmental factors. We refer to homeostasis of the organism in ontogenesis. As we know, the number of kernels formed in a spike depends on genetic information and conditions under which the stages of organogenesis take place. Starting with the primordial stage of spike elements and ending with the stages of florescence and kernel formation, the genotype constantly interacts with numerous environmental factors. Consequently, the more sensitive the genotype to the factors that are of first and foremost importance to formation of spike elements, the higher phenotypic variability of the character under study should be.

Hence we have the second cause, duration of development of the ontogenetic stages related to establishment and formation of spike elements. Of course, the dynamics of meteorological factors during the vegetation period are important. With the acute shortage of water in July 1974, the genotypes with a long vegetation period were more susceptible to the adverse effect of drought and this, in turn, led to increased phenotypic variability of the trait. The foregoing is illustrated by the fact that early ripening cultivar Ac and hybrids derived from it, which differ from other cultivars and hybrids in that they have a shorter vegetation period, are characterized by relatively low phenotypic variability of kernels per spike.

The third cause, which we cannot rule out, is the degree of genotypic heterogeneity of cultivars, not only with respect to number of kernels per spike, but all traits related to morphofunctional ontogenetic inception of spike elements. Of the 7 cultivars studied, only 2 (S29, M553) were tested for heterogeneity before use in crosses by breaking them down into lines that were tested under different vegetation conditions. It was shown that M553 is characterized by some heterogeneity of rate of development and this, in turn, affected phenotypic manifestation of other quantitative characters. No appreciable heterogeneity for quantitative traits was demonstrated in cultivar S29.

In 1973, all nonlocal cultivars, with the exception of Ac had lower values for variances than local cultivar M553, and this applied to only 2 in 1974 (IBO, P62). The fact that there was a drastic drop in variance value, as

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compared to the parents, in F_1 serves as evidence in part that the main cause of high phenotypic variability of the trait under study is not intravarietal heterogeneity.

Thus, on the basis of the obtained results, it is assumed that phenotypic variability of the trait in cultivars is related mainly to sensitivity of the genetic system of control of the character to environmental conditions in the course of the vegetation period on the experimental plot. Since the submitted sets of variable values were obtained as a result of combining data for four blocks, the differences between which were proven by variance analysis, obviously the variances analyzed reflect variability of the character when plants are raised, not only on the plot, but variability that arises when they are raised in different blocks.

From the breeding point of view, of greatest value are the parents that yield hybrids with positive transgressive segregation in F_2 . As shown by the vertical lines covering classes of original parents (see Tables 6 and 7), there was segregation of a negligible number of plants with more kernels than the best parent plants in hybrid Dw×M553 in 1973 and P62×M553 in 1974.

This is apparently related, first of all, to the fact that one of the parents is characterized by high phenotypic variability; for this reason, against this background it is extremely difficult under field conditions to fix genotypes in segregating populations that have a higher genetic potential for number of kernels per spike than the parents.

According to the results of analysis of nature of expression and inheritance of the trait under different vegetation conditions, of the 7 cultivars tested, foreign cultivar Dw, semidwarfs P62 and IB0, and the Siberian tall cultivar M553 are of greatest breeding value. Relatively effective selection in segregating generations is expected from hybrid combinations Dw×M553, P62×M553 and IB0×M553.

The author wishes to express his sincere gratitude to S. A. Sadykova, K. Ye. Shnayder and Ye. Ya. Reger for their technical assistance with the experiment.

Conclusions

The cultivars studied differ appreciably in nature of expression and inheritance of number of kernels per spike. This trait is controlled mainly by genes with additive action, some genes manifesting dominant and overdominant effects that are strongly modified by environmental conditions.

Positive transgressive segregation was manifested only in hybrid Dw×M553 in 1973 and P62×M553 in 1974. There was no expression of transgression in F_2 for the other hybrids.

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This trait is characterized by high phenotypic variability, which is related to the sensitivity of the genetic system of control thereof to environmental factors during ontogenesis.

It is expected that selection for number of kernels per spike will be relatively effective in segregating generations of P62×M553, IB0×M553 and Dw×M553 hybrids.

There are 7 tables; bibliography lists 17 items.

BIBLIOGRAPHY

1. Hsu, P., and Walton, P. D. "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54.
2. Rachinski, T. "Inheritance of Culm Height and Spike Productivity in Intervarietal Soft Wheat Hybrids," GENETIKA I SELEKTSIA (NRB) [Genetics and Breeding (in Bulgarian)], Vol 4, No 6, 1971, 369.
3. Zonic, J., and Jovanovic, B. "Heritability and Correlations of Some Components of Yield in Two Wheat Hybrids," "Eucarpia. Proceedings Meeting Sec. Cereals on Physiol.," Dijon, 1970 (1971), p 365.
4. Jain, R. P., and Aulakh, H. S. "Variability in Wheat (Triticum aestivum L.)," INDIAN J. AGRIC. SCI., Vol 31, No 4, 1971, 297.
5. Reyter, B. G., and Leont'yev, S. I. "Heritability of Some Quantitative Characters and Genetic Effect of Selection in Hybrid Spring Wheat Populations," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1972, 44.
6. Tikka, S. B. S.; Jaimini, S. N.; and Goyal, S. N. "Variability Studies in Wheat Under 'Barani' Conditions," SCI. AND CULT., Vol 39, No 3, 1973, 129.
7. Rajinder, K.; Anand, S. C.; and Virk, D. S. "Heritability and Genetic Advance of Some Quantitative Characters in Crosses of Wheat (Triticum aestivum L.)," J. RES., Vol 9, No 4, 1972, 515.
8. Akhmedova, E. G. "Inheritance of Quantitative Characters in Ecologically Remoted First Generation Hybrids in Karabakh," "Tr. in-ta genetiki i selektsii AN AzSSR" [Works of the Institute of Genetics and Breeding, Azerbaijan Academy of Sciences], No 6, 1970, 118.
9. Sandhu, T. S., and Singh, G. "Studies on Expression of Heterosis in Wheat," INDIAN J. AGRIC. SCI., Vol 37, No 6, 1967, 544.

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10. Dimova, R. "Heterosis in Wheat," "Nauchnyye tr. Vissh. Selskoston. in-t, Dimitrov, Agronom. f-t, ser. rasteniyevodstvo" [Scientific Works of the Higher Agricultural Institute imeni G. Dimitrov, Agronomy Faculty, Plant-Growing Series (Bulgarian)], No 19, 1968, 127.
11. Lubnin, A. N. "Heterosis and Inheritance of the Main Breeding Characters in F₁ From Crosses of Certain Winter Wheat Cultivars," BYUL. VNII RASTENIYEVODSTVA [Bulletin of the All-Union Scientific Research Institute of Plant Growing], Vyp 32, 1973, 10.
12. Singh, J., and Anand, S. C. "Inheritance of Grain Number in Wheat," INDIAN J. GENET. AND PLANT BREED., Vol 31, No 1, 1971, 177.
13. Orlyuk, A. P. "Transgression of Quantitative Characters in Winter Wheat Hybrids," TSITOLOGIYA I GENETIKA [Cytology and Genetics], Vol 6, No 1, 1972, 52.
14. Tsil'ke, R. A. "Variability of Nature of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIB. VESTN. S.-KH. NAUKI, No 2, 1974, 31.
15. Idem, "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses, Report 1: Stem Length," GENETIKA [Genetics], Vol 11, No 2, 1975, 14.
16. Fontdevila, A. "Genotype-Temperature Interaction in Drosophila Melanogaster. II: Body Weight," GENETICS, Vol 73, No 1, 1973, 125.
17. Gustafsson, A., and Dormling, I. "Dominance and Overdominance in Phytotron Analysis of Monohybrid Barley," HEREDITAS, Vol 70, No 2, 1972, 185.
[485-10,657]

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STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 6: WEIGHT PER 1000 KERNELS

Moscow GENETIKA in Russian Vol 13, No 12, 1977 pp 2087-2096

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Siberian Department of All-Union Academy of Agricultural Science imeni Lenin, Omsk, submitted 7 Sep 76]

[Text] Introduction

Kernel size is of agronomic importance, so that much attention is devoted to this character in breeding programs. The main index of size is the weight of 1 or 1000 kernels. It is known that spike productivity is closely related to weight per 1000 kernels. The world wide pool of soft wheat genes is characterized by considerable diversity of this trait. The degree of expression of this character depends on the genotype and environmental conditions, under which the kernel is formed and develops.

Studies have shown that the trait is controlled by many genes with different types of action and interaction. Diallelic analysis established that a significant part of genotypic variability is due to the additive action of genes [1]. However, unlike a number of other quantitative traits that determine spike productivity, there is particularly distinct expression of varying degrees of dominance and overdominance in weight per 1000 grains [2, 3]. It has been demonstrated that there is nonallelic gene interaction in some cultivars used in diallele crosses [4]. An appreciable heterotic effect in kernel size was obtained in many hybrid combinations [5-8], while no heterosis was expressed in some F₁ hybrids [9]. In most studies high indices of heritability of the trait, in the broad sense, were obtained [10-18]. On this basis, it is generally concluded that selection for kernel size in segregating generations is highly effective. However, it should be noted that a significant share of genotypic variability of this character is related to expression of an overdominant effect due to heterozygosity of loci that control processes of caryopsis formation. Since this effect is not fixed by selection and, for this reason, has no breeding significance in self-pollinating plants, a stricter approach should be used to evaluation of the nature of inheritance of the trait in

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order to reliably predict the effectiveness of selection in segregating generations of hybrids for large kernels.

In this article, we report the results of a study of nature of expression and inheritance of weight per 100 kernels in soft spring wheat topcrosses.

Material and Methods

As maternal parents we used foreign cultivars: Dwarf S₆₉₆A-7 (Dw), IBO-3048-433 (IBO), Pitic 62 (P62), Acadia (Ac) and Gun To-may (Gt), seeds of which were obtained from the collection of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov (VIR). Cultivars Saratovskaya 29 (S29) and Mil'turum 553 (M553), raised extensively in Siberia, served as the paternal plants (testers). A detailed description of the cultivars and information about methods used in the experiment, as well as vegetation conditions are submitted in our first and second reports [19, 20].

Experimental Section and Discussion

The results of variance analysis listed in Table 1 indicate that differences are reliable, not only between variants (parents and hybrids), but between replications. It should be noted that the mean square for the variants was 1.5 times higher in 1973 than 1974, whereas the mean square for replications was 3.5 times higher in 1974 than 1973. The mean squares for interaction (A×B) and random deviations did not change appreciably under different vegetation conditions.

Table 1. Results of variance analysis

Source of variability	1973			1974		
	df	ms	F	df	ms	F
Variant, A	26	2159.90	82.22 *	26	1617.55	57.24 *
Replication, B	3	467.12	17.78 *	3	1040.05	58.27 *
A×B interaction	78	63.12	2.40 *	78	65.43	2.32 *
Random deviations	2062	26.27	—	5078	28.28	—

* P<0.001.

Table 2. Weight per 1000 kernels in parents and hybrids ($\bar{x} \pm s_{\bar{x}}$), g

Culti- var, hybrid	1973					1974				
	P	S 29		M 553		P	S 29		M 553	
		F ₁	F ₂	F ₁	F ₂		F ₁	F ₂	F ₁	F ₂
Dw	26.63±0.57	40.01±0.33	37.39±0.89	39.35±0.43	36.92±1.12	38.59±0.41	39.18±0.40	36.79±0.35	38.27±0.43	36.10±0.37
P 62	31.33±0.47	40.86±0.41	38.48±0.81	39.91±0.40	36.02±0.59	35.30±0.52	36.24±0.39	35.09±0.26	35.99±0.33	32.89±0.27
IBO	40.82±0.54	51.79±0.40	43.90±0.76	44.13±0.58	39.79±0.94	32.26±0.38	41.18±0.32	38.16±0.37	41.82±0.58	34.96±0.81
Gt	40.56±0.57	48.92±0.36	45.28±0.56	43.90±0.42	38.20±0.62	41.54±0.32	44.72±0.27	42.46±0.29	39.75±0.42	33.16±0.34
Ac	41.62±0.43	44.97±0.43	43.42±0.69	43.32±0.36	39.38±0.65	35.88±0.29	40.40±0.30	38.40±0.24	39.34±0.28	30.06±0.22
M 553	32.02±0.57	—	—	—	—	34.99±0.29	—	—	—	—
S 29	42.00±0.38	—	—	—	—	41.78±0.34	—	—	—	—
1 ₂	36.42	45.31	41.69	42.13	37.98	37.09	40.34	38.10	39.03	35.64

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The data in Table 2 indicate that the parent cultivars differ significantly in weight per 1000 kernels. In 1973, weight per 1000 kernels ranged from 26.63 (Dw) to 41.62 (Ac) among the foreign cultivars used as maternal parents and in 1974 it ranged from 32.26 (IBO) to 41.54 (Gt). As we see, a strong interaction was manifested between varietal genotype and vegetation conditions. While the smallest kernel was formed in Dw in 1973, this applied to IBO in 1974. In 1973, cultivars IBO, Gt and Ac did not differ reliably in weight per 1000 kernels, whereas in 1973 Gt was considerably superior to the other nonlocal cultivars with regard to this trait. There was also a substantial difference between cultivars S29 and M553, which are raised so extensively in Siberia. In 1973, the weight per 1000 kernels was 9.98 g higher in S29 than M553 and in 1974 it was 6.39 g higher.

The group means (\bar{x}_0) indicate that, on the whole, the hybrids formed larger kernels than the base varieties, and the weight per 1000 kernels dropped in F_2 hybrids, as compared to F_1 , which is indicative of the significant contribution of heterozygosity to genetic control of the character in F_1 hybrids.

In 1973, for hybrids involving tester S29, the weight per 1000 kernels ranged from 30.01 (Dw×S29) to 51.79 (IBO×S29) in F_1 and from 37.39 (Dw×S29) to 45.28 g (Gt×S29) in F_2 ; for hybrids derived from tester M553, the range was from 38.35 (Dw×M553) to 44.15 (IBO×M553) in F_1 and 36.02 (P62×M553) to 39.39 g (IBO×M553) in F_2 . In 1974, for hybrids derived from tester S29 this index ranged from 36.24 (P62×S29) to 44.72 (Gt×S29) in F_1 and 35.09 (P62×S29) to 42.48 g (Gt×S29) in F_2 ; for hybrids derived from tester M553, the range was from 35.99 (P62×M553) to 41.82 (IBO×M553) in F_1 and 32.89 (P62×M553) to 38.16 (Gt×M553) in F_2 . As we see, genotype × environment interaction was also expressed in the hybrids, though not as strongly as in the cultivars. We were impressed by the fact that the group means for the hybrids derived from tester M553 were close to the means for hybrids involving S29, although the former tester has a significantly lower weight per 1000 kernels. This indicates that cultivars S29 and M553 are characterized by about the same general combining ability for the trait under study, even though they themselves differ appreciably in expression of this trait.

Table 3 lists estimates of dominance calculated by two methods [21, 22]. In 1973, there was expression of overdominance in 3 hybrids involving tester S29 (Ac×S29, IBO×S29, Gt×S29) and all hybrids involving M553 in F_1 , and incomplete dominance of the parent with larger weight per 1000 kernels in 2 hybrids (P62×S29, Dw×S29). In 1974, there was expression of overdominance in F_1 of 3 hybrids (Gt×S29, Ac×M553, IBO×M553) and virtually complete dominance of the parent with lower weight per 1000 kernels in 1 hybrid (P62×S29). In 3 hybrids (Dw×S29, Dw×M553, Gt×M553), the mean value in F_1 did not differ reliably from the mean between parents; however, there are no grounds to consider intermediate inheritance here, since the Dw×S29 F_1 hybrid is closer to the parent with less expression of the trait,

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while Dw×M553 and Gt×M553 hybrids are closer to the one with greater expression. The obtained estimates thus indicate that there are significant dominant and overdominant effects of genes that control the weight per 1000 kernels in the material studied, the degree and direction of these effects being significantly modified by environmental conditions.

Table 3. Results of estimation of dominance (D) in F₁

Hybrid	1973				1974			
	S 29		M 553		S 29		M 553	
	D'	D''	D'	D''	D'	D''	D'	D''
Ac	3.16 **	>200.0	6.5 **	117.7	1.92 *	83.1	4.06 **	>200.0
IBO	10.38 **	>200.0	7.73 **	137.5	4.36 **	97.8	8.20 **	>200.0
P62	4.20 **	89.0	8.23 **	>200.0	-2.10 *	15.5	0.85	>200.0
Dw	5.69 **	87.0	10.03 **	>200.0	-0.81	21.1	1.48	91.1
Gt	7.04 **	>200.0	7.61 **	139.1	3.26 **	>200.0	1.49	72.7

Note: Differences are reliable with: *P<0.01 and **P<0.001.

D' refers to estimate made according to Fontdevila [21] and

D'' to estimate made according to Gustafsson and Dormling [22].

Table 4. Deviation of F₁ and F₂ hybrids from best parent

Hybrid	1973								1974							
	S 29				M 553				S 29				M 553			
	F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		F ₁		F ₂	
	r	%	r	%	r	%	r	%	r	%	r	%	r	%	r	%
Ac	2.97 ***	7.0	1.42	3.4	1.70 *	4.1	-2.24 **	5.4	-0.98	2.4	-2.98 ***	7.2	3.76 ***	10.6	0.48	1.3
IBO	9.79 ***	23.3	1.90 *	4.5	3.23 **	8.2	-1.43	3.5	-0.20	0.5	-3.22 ***	7.8	6.83 ***	19.5	-0.03	0.1
P62	-1.14	2.7	-3.32 **	8.4	7.89 **	24.6	4.00 ***	12.5	-5.14 ***	12.4	-6.29 ***	15.2	0.69	2.0	-2.41	6.6
Dw	-1.89 *	4.7	-4.61 **	11.0	7.33 **	22.9	4.90 ***	13.5	-2.20 **	5.3	-4.99 ***	12.0	-0.32	0.8	-2.49 **	6.4
Gt	6.92 ***	16.5	3.28 **	7.8	3.34 **	8.2	-2.36 **	5.8	3.18 ***	7.8	0.94	2.3	-1.78 *	4.3	-3.38 ***	8.1

* P<0.05; ** P<0.01; *** P<0.001.

Table 4 lists data on magnitude of heterosis in F₁ and F₂, which are quite consistent with the results of evaluation of dominance (see Table 3). Heterosis was expressed in hybrids that demonstrated overdominance in F₁. In 1973, there was expression of heterosis in weight per 1000 kernels in 3 hybrids involving tester S29 and all those involving M553, ranging from 4.1 (Ac×M553) to 24.6% (P62×M553) in F₁. In 1974, heterosis was expressed in 3 hybrids: Gt×S29 (7.6%), Ac×M553 (10.6%) and IBO×M553 (19.5%). Heterosis was either drastically diminished or lacking in F₂. Typically enough, heterosis diminished to one-half in F₂ of the level in F₁ in 4 hybrids in 1973 (Ac×S29, Gt×S29, P62×M553 and Dw×M553). These results clearly indicate that, in these hybrids, heterosis is related to heterozygosity of loci controlling the weight per 1000 kernels in F₁.

APPROVED FOR RELEASE: 2007/02/08: CIA-RDP82-00850R000200050036-5

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in view of the fact that there is expression of substantial heterosis for the trait under study, due to heterozygosity of loci, the coefficients of heritability in the broad sense will include genotypic variability, which it is impossible to fix by selection (overdominance); therefore, this index cannot serve as a reliable criterion to predict the effectiveness of selection in early segregating generations.

Table 5. Value of variance (σ^2) for parents and hybrids

Cultivar & hybrid	1973					1974				
	P	S 29		M 553		P	S 29		M 553	
		F ₁	F ₂	F ₁	F ₂		F ₁	F ₂	F ₁	F ₂
Dw	26.2	8.8	63.2	14.6	100.8	20.9	19.4	43.3	19.6	43.9
IBO	23.5	13.1	46.6	26.9	71.5	16.6	12.9	40.6	21.3	111.9
P 62	17.5	13.2	30.2	12.6	28.1	18.0	19.2	22.3	12.2	25.4
Ac	15.1	14.6	38.4	10.5	33.0	10.7	11.7	16.9	9.6	15.9
Gt	25.7	10.0	24.8	14.3	30.8	11.7	8.9	28.3	21.1	37.4
S 29	11.3	—	—	—	—	14.8	—	—	—	—
M 553	25.8	—	—	—	—	10.9	—	—	—	—

The variances characterizing phenotypic variability of the character in parents, F₁ and F₂ hybrids indicate that the relative share of genotypic variability in F₂ of most hybrids is rather high; but since a significant part thereof is induced by overdominance, the coefficients of heritability in the broad sense are not calculated (Table 5). Unlike other quantitative characters of the spike, the variance for weight per 1000 kernels undergoes less fluctuation in the 2 years. In 1973, variance ranged from 11.3 (S29) to 26.2 (Dw) and in 1974 from 10.7 (Ac) to 20.9 (Dw) in the cultivars. In the hybrids, this index ranged from 8.8 (Dw×S29) to 26.9 (IBO×M553) in F₁ and 24.8 (Gt×S29) to 100.8 (Dw×M553) in F₂ in 1973, from 8.9 (Gt×S29) to 21.3 (IBO×M553) in F₁ and 15.9 (Ac×M553) to 111.9 (IBO×M553) in F₂ in 1974. These data indicate that there was a drastic increase in phenotypic variability of the trait as a result of segregation; however, a significant part of this variability is induced by segregation of heterozygotic and homozygotic genotypes differing markedly in phenotypic expression of the character.

Variational series (Tables 6 and 7) yield fuller information about the nature of variability of the character in parents and hybrids. On the whole, it should be noted that the distribution of plants according to weight per 1000 kernels is close to normal, not only in parents and F₁ hybrids, but in F₂ hybrids. The bimodal distribution of plants observed in 1973 for cultivar IBO and F₂ of hybrids Dw×M553 and IBO×M553 is apparently related to the small size of the sample (n = 80) and sensitivity of the character to environmental conditions. Although the mean values for the trait differ reliably in most parents used in crosses, there is almost complete overlapping of the sets of variable values. This was particularly evident in 1974, when the differences between genotypes leveled off, as compared to 1973, which was related to an acute shortage of water and high temperatures in July. This speeded up kernel formation in all cultivars and hybrids.

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Table 6. Distribution of parent, F₁ and F₂ hybrid plants according to wt./1000 kernels in 1973, %

Class	Dw x M33		Ac x M33		Gt x M33		Dw x M33		Ac x M33		Gt x M33		Dw x M33		Ac x M33		Gt x M33		Dw x M33		Ac x M33		Gt x M33	
	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q
11-13	1																							
14-16	4	3	1																					
17-19	14	1	1																					
20-22	23	18	1	1																				
23-25	26	28	6	1																				
26-28	29	31	26	10	43	1																		
29-31	32	34	2	6	4																			
32-34	33	37	2	6	4																			
35-37	38	40	1	11	18	21	6	3																
38-40	41	43	1	28	61	34	36	1	43	13	31	12												
41-43	44	46	1	21	1	29	28	25	3	11	9	14	10											
44-46	47	49	4																					
47-49	50	52																						
50-52	53	55																						
53-55	56	58																						
56-58	59	61																						
59-61	62	64																						
62-64	65	67																						
65-67																								

Note: Here and in Table 7, boldface vertical line refers to maternal classes and dotted line to paternal ones.

Table 7. Distribution of parent, F₁ and F₂ hybrid plants according to wt./1000 kernels in 1974, %

Class	Dw x M33		Ac x M33		Gt x M33		Dw x M33		Ac x M33		Gt x M33		Dw x M33		Ac x M33		Gt x M33		Dw x M33		Ac x M33		Gt x M33	
	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q	q
8-10	1																							
11-13	1																							
14-16	1																							
17-19	2	5	4	2																				
20-22	2	5	4	2																				
23-25	2	5	4	2																				
26-28	2	5	4	2																				
29-31	2	5	4	2																				
32-34	2	5	4	2																				
35-37	2	5	4	2																				
38-40	2	5	4	2																				
41-43	2	5	4	2																				
44-46	2	5	4	2																				
47-49	2	5	4	2																				
50-52	2	5	4	2																				
53-55	2	5	4	2																				

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Of particular breeding value are the hybrid combinations that present positive transgression in segregating generations for elements that determine spike productivity. In 1973, significant transgressive segregation in F_2 (19%) for weight per 1000 kernels was expressed only in hybrid $Dw \times M553$. Typically enough, in 1973 this hybrid also presented the highest variances in F_2 (100.8) and expressed a high heterosis effect in F_1 (22.9%). Consequently, the higher mean value of the trait in F_1 than the mean for the best parent is related not only to overdominance, but other types of action and interaction of genes, the recombination of which leads to segregation of genotypes characterized by higher weight per 1000 kernels in their phenotypic expression than the best parent and F_1 hybrid plants. However, in 1974, no appreciable transgressive segregation was observed in this hybrid, or in the others. This is probably related to the fact that under the more rigorous vegetation conditions there was incomplete expression of genetic information for genotypes in segregating generations.

We were impressed by hybrid $IBO \times S29$, in F_2 of which there was expression of transgressive segregation, i.e., 8% of the plants formed larger kernels than the best S29 parent. But if we analyze the distribution of F_1 plants, we see that more than half of them (52%) formed a heavier kernel than the best parent. This is indicative of pseudotransgression, which is often not considered in studies of this phenomenon. When analyzing transgressive segregation, one must not overlook the nature of expression of the character in F_1 . By comparing the results of segregation in F_2 only to the original parents, one can arrive at a fallacious conclusion and make the wrong prediction of effectiveness of selection in segregating generations.

In summing up the results obtained on nature of expression and inheritance of weight per 1000 kernels, we must call attention to the following points: It was demonstrated that genes with additive action make a substantial contribution to the genetic system of control of the trait, and strong interaction is observed between the genotypes and environment. This applies primarily to the foreign cultivars. Unlike other quantitative characters of the head (length, number of kernels, number of spikelets), considerable dominant and overdominant effects are expressed for weight per 1000 kernels, which are strongly modified by the conditions under which the kernels are formed.

It was established that there is no expression of positive transgressive segregation for kernel size in most hybrids studied. The high phenotypic variability of the trait in F_2 is related mainly to dominant and overdominant effects; for this reason, one should not calculate the coefficients of heritability in the general sense, since they cannot serve as a reliable criterion to predict selection in segregating generations. In the hybrid combinations that express overdominance, selection for kernel size should begin in F_3 and F_4 . In view of these distinctions, hybrids $Gt \times S29$ and $Dw \times M553$ are the most valuable ones for practical breeding to enlarge the kernel.

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The author wishes to express his sincere gratitude to S. A. Sadykova, L. K. Getman, K. Ye. Shnayder and Ye. Ya. Reger for their technical assistance with the experiment.

Conclusions

This study revealed that cultivars differ appreciably in nature of manifestation and inheritance of weight per 1000 kernels. This trait is controlled by a complex genetic system which interacts strongly with environmental conditions.

In addition to the additive action of genes, genes with dominant and overdominant effects make a significant contribution to genetic variability of the character. Overdominance was expressed in 8 hybrids in 1973 and 3 out of 10 in F_1 in 1974. The rest of the hybrids presented varying degrees of dominance in the direction of the parent with heavier weight per 1000 kernels, with the exception of hybrid P62×S29, in which there was virtually complete dominance of the parent with lower weight per 1000 kernels.

Heterosis was manifested in 8 hybrids ($4.1 \pm 24.6\%$) in 1973 and 3 ($7.6 \pm 19.5\%$) in 1974).

In view of the fact that a significant overdominant effect is observed for the character in question, one should begin selection in F_3 and F_4 . It is expected that selection among Gt×S29 and Dw×M553 hybrids will be the most effective.

There are 7 tables; bibliography lists 22 items.

BIBLIOGRAPHY

1. Hsu, P., and Walton, P. D. "The Inheritance of Morphological and Agronomic Characters in Spring Wheat," EUPHYTICA, Vol 19, No 1, 1970, 54.
2. Brown, C. M.; Weibel, R. O.; and Seif, R. D. "Heterosis and Combining Ability in Common Wheat," CROP SCI., Vol 6, No 6, 1966, 382.
3. Chapman, S. R., and McNeal, F. H. "Gene Action for Yield Components and Plant Height in a Spring Wheat Cross," Ibid, Vol 11, No 3, 1971, 384.
4. Kalashnik, N. A., and Molin, V. I. "Genetic Control of Quantitative Characters in Spring Wheat," GENETIKA [Genetics], Vol 10, No 11, 1974, 17.
5. Lubnin, A. N. "Heterosis and Inheritance of the Main Breeding Characters in F_1 of Some Winter Wheat Crosses," BYUL. VNII RASTENIYEVODSTVA [Bulletin of the All-Union Scientific Research Institute of Plant Growing], Vyp 32, 1973, 10.

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6. Lyfenko, S. F., and Kovbasenko, G. M. "Distinctive Features in Inheritance of Economically Useful Characters in Soft Winter Wheat Hybrids," VESTN. S.-KH. NAUKI [Vestnik of Agricultural Science], No 8, 1970, 20.
7. Sandhu, T. S., and Singh, G. "Studies on Expression of Heterosis in Wheat," INDIAN J. AGRIC. SCI., Vol 37, No 6, 1967, 544.
8. Grant, M. N., and McKenzie, H. "Heterosis in F₁ Hybrids Between Spring and Winter Wheats," CANAD. J. PLANT SCIENCE, Vol 50, No 2, 1970, 137.
9. Rai, R. K.; Stoskopf, N. C.; and Reinbergs, E. "Studies With Hybrid Wheat in Ontario," Ibid, Vol 50, No 4, 1970, 485.
10. Mamonov, L. K. "Effect of Genotype and Seasonal Conditions on Some Indices of Structure of Spring Wheat Yield," GENETIKA, Vol 6, No 9, 1970, 23.
11. Jain, R. P., and Aulakh, H. S. "Variability in Wheat (Triticum aestivum L.)," IND. J. AGRIC. SCI., Vol 41, No 4, 1971, 297.
12. Rachinski, T. "Inheritance of Culm Height and Spike Productivity in Intervarietal Soft Wheat Hybrids," GENETIKA I SELEKTSIYA [Genetics and Breeding (Bulgarian)], Vol 4, No 6, 1971, 369.
13. Reyter, B. G., and Leont'yev, S. I. "Heritability of Some Quantitative Characters and Genetic Effect of Selection in Hybrid Spring Wheat Populations," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1972, 44.
14. Khadr, F. H.; Ismail, A. M.; and Morsy, M. S. "Heritabilities of Quantitative Traits Estimated by Different Methods in Generations of Wheat Crosses," EGYPT. J. GENET. AND CYTOL., Vol 1, No 2, 1972, 263.
15. Rajinder, K.; Anand, S. C.; and Virk, D. S. "Heritability and Genetic Advance of Some Quantitative Characters in Crosses of Wheat (Triticum aestivum L.)," J. RES., Vol 9, No 4, 1972, 515.
16. Tikka, S. B. S.; Jaimini, S. N.; and Goyal, S. N. "Variability Studies in Wheat Under 'Barani' Conditions," SCI. AND CULTURE, Vol 39, No 3, 1973, 129.
17. Smocek, J., and Kristof, Z. "Expression of Inheritance and Correlation Between Characters in Wheat Hybrids," GENET. A SLECHT. [Genetics and Plant Breeding (Czech)], Vol 11, No 2, 1975, 105.

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18. Reddy, M. V.; Heyne, E. G.; and Liang, G. H. L. "Heritabilities and Interrelations of Shortness and Other Agronomic Characters in F₃ and F₄ Generations of Two Wheat Crosses (*Triticum aestivum* L. em Thell)," CROP SCI., Vol 9, No 2, 1969, 222.
19. Tsil'ke, R. A. "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 1: Stem Length," GENETIKA, Vol 11, No 2, 1975, 14.
20. Idem, "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 2: Duration of Germination-Heading Period," Ibid, Vol 13, No 1, 1977, 5.
21. Fontdevila, A. "Genotype-Temperature Interaction in *Drosophila Melanogaster*. 2: Body Weight," GENETICS, Vol 73, No 1, 1973, 125.
22. Gustafsson, A., and Dormling, I. "Dominance and Overdominance in Phytotron Analysis of Monohybrid Barley," HEREDITAS, Vol 70, No 2, 1972, 185.
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STUDY OF INHERITANCE OF QUANTITATIVE CHARACTERS IN SOFT SPRING WHEAT
TOPCROSSES. REPORT 7: KERNEL WEIGHT PER SPIKE

Moscow GENETIKA in Russian Vol 14, No 1, 1978 pp 15-24

[Article by R. A. Tsil'ke, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 9 Nov 76]

[Text] Introduction

Wheat yield per unit area planted is directly composed of two elements: kernel weight per spike and number of productive heads. The intensity of these two yield elements depends on genetic information contained in the genotype and numerous factors in the environment in which the plant grows. Since spike grain weight reflects the overall expression of several characters, each of which is controlled by a large number of genes that function under specific endogenous and exogenous conditions, the researcher encounters methodological difficulties when studying the nature of inheritance of this complex trait. Spike productivity is directly related to number of kernels per spike and weight per kernel. In turn, the number of kernels is related to number of spikelets per spike and kernels per spikelet. There is no need to break down even more these elements of the spike. Let us merely indicate that each of them constitutes a complex morphofunctional system, which interacts closely with environmental conditions at all stages of ontogenesis.

As was to be expected, weight of kernels per spike is controlled by many genes with different types of action and interaction [1-13].

It has been reported [1] that kernel weight per spike is controlled mainly by genes with additive action, those with dominant and overdominant effects playing a lesser role. Other works [2-4] indicate that dominance and overdominance have an appreciable influence on intensity of the trait in hybrids. Transgressive segregation in F_2 of some hybrid combinations has been observed for spike productivity [5-7].

Some studies [3, 5, 8, 9] reported high heritability of the character, while others [10, 11] found it low. As a rule, negligible heterosis is expressed

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with regard to grain weight [1, 6, 12, 13]. In most studies, it was found that the nature of expression and inheritance of head productivity are strongly related to genotypic differences between hybridized parents and environmental conditions.

Few studies of the nature of inheritance of spike productivity have been conducted in Siberia [8, 11], although such information is extremely necessary to develop effective breeding programs.

We report here the results of an experimental study of the nature of inheritance of weight of kernels per spike in soft spring wheat topcrosses.

Material and Methods

We used as maternal plants five foreign cultivars obtained from the collection of the All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov: Dwarf S696 A-7 (Dw), IBO-3048-433 (IBO), Pitic 62 (P62), Acadia (Ac) and Gun To-may (Gt). Cultivars Saratovskaya 29 (S29) and Mil'turum 553 (M553), which are raised extensively in Siberia, served as the paternal parents (testers). Each cultivar used in the experiment is characterized by some unique traits or a set of economically valuable ones: unlike most known short-stemmed cultivars, Dw forms a long head with many spikelets; IBO is exceptionally resistant to lodging, is not stricken by powdery mildew and mildly susceptible to brown rust; P62 is an intensive type of cultivar that is very responsive to a high fertility of soil; Ac is drought resistant and forms grain with high baking qualities; Gt forms a highly productive head; S29 is notable for excellent kernel quality and high homeostasis; M553 is adapted to local conditions. In 1973, we analyzed 80 specimens of each cultivar, F₁ and F₂ hybrids; in 1974, we analyzed 80 specimens of cultivars and F₁ hybrids, and 320 of F₂. Additional information about the base material and experimental methods is given in our first and second reports [14, 15].

Experimental Section and Discussion

The results of variance analysis listed in Table 1 indicate that the differences in kernel weight per spike are significant ($P < 0.001$) not only between variants (parents and hybrids), but between replications. In 1974, the mean squares (ms) were greater for variants, A×B interaction and random deviations than in 1973. The mean square was 1.5 times greater for variants in 1974 than 1973, i.e., there was more marked difference between genotypes in the former case.

Table 2 lists experimental data on weight of kernels per spike in parents and hybrids. On the whole, the cultivars and hybrids formed a more productive head in 1973 than in 1974. In 1973, the weight of kernels per spike for nonlocal cultivars used as maternal parents ranged from 0.90 (Dw) to 1.60 (IBO) and in 1974 from 0.74 (Ac) to 1.50 g (Gt). These data indicate that there was expression of strong genotype × environment

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interaction. Typically enough, under the more clement vegetation conditions (1973), the locally grown cultivar S29 was significantly superior to the other local one, M553, in weight of kernels per spike (the difference constituted 0.44 g). In 1974, when there was an acute shortage of water in July, the differences between these cultivars were unreliable. The differences between P62 and Gt were also unreliable in the 2 years. In 1973, in hybrids derived from tester S29 the weight of kernels per spike ranged from 1.22 g (Ac×S29) to 1.50 (P62×S29) in F₁ and 1.18 (Ac×S29) to 1.40 (Gt×S29; IBO×S29) in F₂, while in hybrids involving tester M553 the weight ranged from 1.03 g (Ac×M553) to 1.64 (Gt×M553) in F₁ and 1.00 (Ac×M553) to 1.37 (P62×M553) in F₂. In 1974, kernel weight per spike ranged from 1.06 (Ac×S29) to 1.36 (Gt×S29) in F₁ and 0.97 (Ac×S29) to 1.24 (Gt×S29) in F₂ of hybrids involving tester S29; the figures for hybrids involving tester M553 were 0.92 (Ac×M553) to 1.62 (IBO×M553) in F₁ and 0.88 (Ac×M553) to 1.26 g (IBO×M553) in F₂. As we see, early ripening cultivar Ac and hybrids derived from it, as well as late ripening dwarf Dw, formed the least productive head. As shown by the group means (\bar{x}_0), hybrids derived from Siberian cultivar M553 generally formed a more productive spike than those derived from the widely raised cultivar S29. We were impressed by the fact that, even in 1973 when M553 was substantially inferior to S29, hybrids involving the former developed a more productive head than those derived from the latter.

Table 1. Results of variance analysis of variability of kernel weight per spike in hybrids and initial cultivars

Source of variability	1973			1974		
	df	ms	F	df	ms	F
Variant (A)	26	3.63	38.30 *	26	5.60	48.67 *
Replication (B)	3	1.60	16.00 *	3	1.30	10.83 *
A×B interaction	78	0.27	2.70 *	78	0.29	2.42 *
Random deviations	2052	0.10	—	5077	0.12	—

* $P < 0.001$.

Table 2. Kernel weight per spike in parents and hybrids, g ($\bar{x} \pm s_{\bar{x}}$)

Maternal form, tester	1973					1974					
	paternal form					paternal form					
	S 29		M 553			S 29		M 553			
	P					P					
	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂	F ₁	F ₂			
Dw	0.90±0.03	1.34±0.03	1.21±0.04	1.43±0.03	1.34±0.05	0.83±0.03	1.25±0.03	1.07±0.02	1.32±0.03	1.22±0.02	—
Ac	0.91±0.02	1.22±0.02	1.18±0.03	1.03±0.02	1.00±0.04	0.74±0.02	1.08±0.02	0.97±0.02	0.92±0.02	0.88±0.01	—
P62	1.34±0.03	1.50±0.03	1.33±0.04	1.56±0.03	1.37±0.04	1.30±0.04	1.31±0.03	1.18±0.02	1.31±0.04	1.22±0.02	—
Gt	1.44±0.04	1.46±0.02	1.40±0.03	1.64±0.03	1.28±0.04	1.50±0.03	1.36±0.02	1.24±0.02	1.37±0.04	1.24±0.02	—
IBO	1.00±0.04	1.37±0.02	1.40±0.09	1.54±0.03	1.30±0.03	1.31±0.04	1.28±0.03	1.11±0.02	1.62±0.03	1.26±0.03	—
M 553	0.86±0.03	—	—	—	—	1.20±0.03	—	—	—	—	—
S29	1.30±0.02	—	—	—	—	1.23±0.02	—	—	—	—	—
(\bar{x}_0)	1.19	1.38	1.30	1.45	1.25	1.16	1.25	1.11	1.31	1.16	—

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In 1973, the difference between extreme parental variants constituted 0.70, it was 0.28 in F₁ of hybrids involving tester S29 and 0.22 g in F₂; for hybrids derived from tester M553, the difference constituted 0.61 g in F₁ and 0.37 in F₂. In 1974, the figures were 0.76 for the parents, 0.30, 0.27, 0.70 and 0.38 g for the hybrids. These data indicate that cultivar M553 is characterized not only by higher general, but also higher specific combining ability for spike productivity than S29.

The nature of inheritance depends not only on the type of action and interaction of genes controlling the trait, but the reaction of the genotype as a whole to vegetation conditions. As we have already mentioned, there was expression of significant interaction between the genotype and environment (year) in F₁ and F₂ hybrids and particularly the cultivars, and this, of course, led to a change in nature of inheritance of the character as a function of vegetation conditions. Table 3 lists estimates of dominance made by two methods [16, 17]. F₁ differed reliably from the mean value of the trait between parents in 3 hybrids involving tester S29 and all hybrids involving tester M553 in 1973, 1 and 2 hybrids, respectively, in 1974. This indicates that, along with additive gene action, a substantial role is played by dominance and overdominance in the genetic system of control of the trait; however, they are significantly modified by environmental conditions. This was to be expected, considering the fact that spike productivity is closely related to number of kernels and their size, i.e., traits for which dominant and overdominant effects are expressed.

Table 3. Results of estimation of dominance in F₁ (D)

Maternal form	1973				1974			
	paternal form							
	29		M 553		29		M 553	
	D'	D''	D'	D''	D'	D''	D'	D''
Ac	0.12 *	79.5	0.15 **	>200.0	0.08	65.3	-0.05	39.1
IBO	-0.08	23.3	0.31 ***	91.9	0.01	62.5	0.36 ***	>200.0
P 62	0.18 ***	>200.0	0.46 ***	145.8	0.05	114.3	0.09	140.0
Dw	0.21 ***	110.0	0.61 ***	>200.0	0.22 ***	105.0	0.30 ***	132.4
Gt	0.00	114.3	0.49 ***	131.5	0.00	48.1	0.02	56.7

Note: D' was estimated (in g) according to Fontdevila [16] and D'' (%) according to Gustafsson and Dormling [17]; level of significance: *P<0.05; **P<0.01; ***P<0.001.

Table 4. Deviation of F₁ and F₂ hybrids from best parent (d)

Maternal form	1973												1974											
	paternal form																							
	S 29				M 553				S 29				M 553											
	F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		F ₁		F ₂		F ₁		F ₂					
	r	%	r	%	r	%	r	%	r	%	r	%	r	%	r	%	r	%	r	%				
Ac	-0.08	6.2	-0.12 **	9.2	0.12 **	13.2	0.09	9.9	-0.17 ***	13.8	-0.26 ***	21.1	-0.28 ***	23.3	-0.32 ***	20.7								
IBO	-0.29 ***	18.1	-0.20 ***	12.5	-0.06	3.8	-0.30 ***	18.8	-0.03	2.3	-0.20 ***	15.3	0.31 ***	23.7	0.05	3.8								
P 62	0.16	11.9	-0.01	0.8	0.22 ***	16.4	0.03	2.2	0.01	0.8	-0.12 *	8.2	0.04	3.1	-0.08	6.2								
Dw	0.04	3.1	-0.09	6.9	0.59 ***	85.6	0.44 ***	48.9	0.02	1.6	-0.16 **	13.0	0.12 *	10.0	0.02	1.7								
Gt	0.02	1.4	-0.04	2.8	0.20 ***	13.9	-0.18 ***	12.5	-0.14 **	9.3	-0.26 ***	17.3	-0.13 **	8.7	-0.26 ***	17.3								

* P<0.05; ** P<0.01; *** P<0.001.

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In 1973, there was expression of overdominance in F_1 of 5 hybrids ($P62 \times S29$, $Ac \times M553$, $P62 \times M553$, $Dw \times M553$, $Gt \times M553$), complete dominance in 1 hybrid ($Dw \times S29$) and incomplete dominance in the direction of the parent with higher kernel weight per spike in 2 hybrids ($Ac \times S29$, $IBO \times M553$). F_1 did not deviate reliably from the mean between parents in 2 hybrids ($IBO \times S29$, $Gt \times S29$); however, this is not indicative of intermediate inheritance, since F_1 was closer to the parent with lower value for the trait in 1 case ($IBO \times S29$) and closer to the parent with the higher value in the other ($Gt \times S29$). In 1973, there was expression of overdominance in 2 hybrids ($IBO \times M553$, $Dw \times M553$), intermediate inheritance in 4 ($Ac \times S29$, $IBO \times S29$, $Gt \times S29$, $Gt \times M553$) and complete dominance of the parent with the more productive spike in 3 ($Dw \times S29$, $P62 \times S29$, $P62 \times M553$). In F_1 of one hybrid ($Ac \times M553$), kernel weight was lower than in the parent with lower expression of the trait; however, the difference is unreliable, so that we can refer to dominance of the parent with less expression of the character. It can also be assumed that genes with epistatic effects are involved in the genetic system of control of the trait in this hybrid combination.

Table 4 lists additional information about the nature of inheritance of kernel weight per spike. In 1973, reliable heterosis, which ranged from 13.2 to 65.6%, was expressed in 4 hybrids ($Ac \times M553$, $P62 \times M553$, $Dw \times M553$, $Gt \times M553$). In 1974, heterosis was expressed in 2 hybrids, $IBO \times M553$ (23.7%) and $Dw \times M553$ (10.0%). We were impressed by the fact that heterosis was demonstrated only in hybrids involving Siberian cultivar M553. Analysis of the data in Table 4 shows also that most F_2 hybrids are reliably inferior to F_1 in weight of kernels per spike. This confirms the estimates of dominance (see Table 3), which indicate that most hybrids involving tester M553 express overdominance in F_1 , which is determined by heterozygosity of loci controlling spike productivity.

In order to obtain fuller information about the nature of expression of the character in the cultivars, F_1 and F_2 hybrids, Tables 5 and 6 list the variational series characterizing phenotypic variability of plants according to weight of kernels per spike. If we consider that the trait in question is made up of a complex set of spike elements and, first of all, such as number of kernels and caryopsis, each of which is controlled by a polygenic system, we should expect normal distribution of plants, both parent and F_1 and F_2 hybrids. In actuality, the distribution of plants according to kernel weight was close to normal for all cultivars and hybrids. It should be noted, however, that a negligible deviation of the series from normal distribution, which was observed for some parents and hybrids in 1973, is related to the fact that the sample was not large enough and there were appreciable differences between blocks (replications).

On the whole, we must call attention to the fact that there was expression of high phenotypic variability of kernel weight per spike, and this is related, on the one hand, to the large number of genes controlling the trait, most of which characterized by mild effects, and, on the other hand, sensitivity of the morphofunctional systems of organogenesis to

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environmental factors at all stages of individual plant development. Hence, the more sensitive the genotype to limiting environmental factors and the longer the period of exposure to these factors during the critical stages of development of the plant elements that determine spike productivity, the greater the phenotypic variability of the trait. Under the less favorable vegetation conditions (1974), when water was the limiting factor, and flowering and kernel formation occurred expressly during the period thereof (July), there was extremely great increase in phenotypic variability of the character in cultivars and hybrids.

The data in Tables 5 and 6 indicate that the foreign cultivars IBO, P62, Gt and local cultivar M553 are characterized by an extremely labile system of control of the character, and among hybrids derived from these cultivars there was expression of high phenotypic variability, not only in F_2 but in F_1 . It is important to consider that each variational series included data pertaining to four replications [blocks], so that variability reflects the differences observed between replications, and they were significant.

The high variability of the trait in parents does not enable us to calculate the coefficients of heritability in the broad sense, since these indices are close to zero or else are negative for a number of hybrids. It is not expedient to determine the coefficients of heritability in the broad sense for hybrids, in which heterosis is expressed in F_1 .

In 1973, there was expression of positive transgressive segregation in hybrids Dw×S29, Dw×M553, P62×M553, Ac×S29 and Ac×M553. In view of the marked phenotypic variability of the character in the original parents in 1974, we failed to demonstrate transgressive segregation. It must also be noted that transgression in hybrid Dw×M553 in 1973 was partially related to overdominance. In view of the exceptionally high phenotypic variability of the character as a whole, it is desirable to conduct selection in segregating generations for the traits that have a positive correlation to spike productivity, but that are less sensitive to environmental conditions. We refer, first of all, to such characters as spike length, number of spikelets and kernels per spike, and kernel size. As a rule, the heterosis effect is not manifested for spike length, number of spikelets and kernels per spike, therefore selection can be started in F_2 , whereas heterosis is not uncommon for weight per 1000 kernels and productivity of the spike as a whole; consequently, selection for these characters should be deferred to later generations (F_3 - F_5).

Selection for elements of spike productivity will be more effective when the hybrid population is grown on a plot that is homogeneous in topography and ground cover, with equal area of nutrition for all plants and with a large enough segregating population (5000-10,000 plants).

The author wishes to express his sincere appreciation to S. A. Sadykova, L. K. Getman, K. Ye. Shnayder and Ye. Ya. Reger for their technical assistance with the experiment.

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Table 5. Distribution of parent, F₁ and F₂ hybrid plants according to kernel weight per spike, % (1973)

Classes, g	D ₁ x D ₂			D ₁ x F ₁			D ₁ x F ₂			D ₂ x F ₁			D ₂ x F ₂			F ₁ x F ₂			P ₁ x P ₂			P ₁ x F ₁			P ₁ x F ₂			P ₂ x P ₁			P ₂ x F ₁			P ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F 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₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G ₂ x F ₂			G ₁ x G ₂			G ₁ x F ₁			G ₁ x F ₂			G ₂ x G ₁			G ₂ x F ₁			G<		
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*See Note to Table 5.

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Conclusions

It was demonstrated that the cultivars differ appreciable in degree of expression and nature of inheritance of kernel weight per spike. Along with the additive action of genes in the control of this character, dominance and overdominance, which are strongly modified by environmental conditions, play a significant role. Strong genotype \times year interaction is manifested by hybrids and, particularly, cultivars.

Positive transgressive segregation was found only under clement vegetation conditions (1973) in the following hybrids: Dw \times S20, Dw \times M553, P62 \times M553, Ac \times S29 and Ac \times M553.

The trait is characterized by exceptionally high phenotypic variability, which is related to sensitivity of the genetic system of its control to environmental conditions.

There are 6 tables; bibliography lists 17 items.

BIBLIOGRAPHY

1. Brown, C. M.; Weibel, R. O.; and Seif, R. D. "Heterosis and Combining Ability in Common Wheat," CROP SCI., Vol 6, No 6, 1966, 382.
2. Chapman, S. R., and McNeal, F. H. "Gene Action for Yield Components and Plant Height in a Spring Wheat Cross," Ibid, Vol 11, No 3, 1971, 384.
3. Sun, P. L.; Shands, H. L.; and Forsberg, R. A. "Inheritance of Kernel Weight in Six Spring Wheat Crosses," Ibid, Vol 12, No 1, 1972, 1.
4. Rachinski, T. "Inheritance of Culm Height and Spike Productivity in Intervarietal Soft Wheat Hybrids," GENETIKA I SELEKTSIYA (NRB)[Genetics and Plant Breeding (Bulgarian)], Vol 4, No 6, 1971, 369.
5. Khadr, F. H. "Variability and Covariability for Plant Height, Heading Date and Seed Weight in Wheat Crosses," THEOR. AND APPL. GENETICS, Vol 41, No 3, 1971, 100.
6. Borojevic, S. "Type of Inheritance and Heritability of Quantitative Traits in Hybrids of Different Wheat Cultivars," SAVREMENA POLJOPR. [Modern Agriculture (Croatian)], Vol 13, No 7-8, 1965, 587.
7. Orlyuk, A. P. "Transgression of Quantitative Characters in Winter Wheat Hybrids," TSITOLOGIYA I GENETIKA [Cytology and Genetics], Vol 6, No 1, 1972, 52.

FOR OFFICIAL USE ONLY

8. Reyter, B. G., and Leont'yev, S. I. "Inheritance of Some Quantitative Characters and Genetic Effect of Selection in Hybrid Spring Wheat Populations," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1972, 44.
9. Jain, R. P., and Aulakh, H. S. "Variability in Wheat (*Triticum aestivum* L.)," INDIAN J. AGRIC. SCI., Vol 4, No 4, 1971, 297.
10. Zonic, J., and Jovanovic, B. "Heritability and Correlations of Some Components of Yield in Two Wheat Hybrids," "Eucarpia. Proceeding Meeting Section Cereals and Physiology," Dijon, 1971, p 365.
11. Tsil'ke, R. A. "Variability of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIB. VESTN. S.-KH. NAUKI, No 2, 1974, 31.
12. Lubnin, A. N. "Heterosis and Inheritance of the Main Breeding Traits in F₁ From Crosses of Some Winter Wheat Cultivars," BYUL. VSES. N.-I. IN-TA RASTENIYEVODSTVA [Bulletin of the All-Union Scientific Research Institute of Plant Growing], Vyp 32, 1973, 10.
13. Villanueva, N. R. "Inheritance of Height and Other Characters Under Conditions of the Coast of Peru," "Proceedings 3th International Wheat Genetics Symposium," Columbia, 1973, p 611.
14. Tsil'ke, R. A. "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 1: Stem Length," GENETIKA [Genetics], Vol 11, No 2, 1975, 14.
15. Idem, "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 2: Duration of Germination-Heading Period," Ibid, Vol 13, No 1, 1977, 5.
16. Fontdevila, A. "Genotype-Temperature Interaction in *Drosophila Melanogaster*. 2: Body Weight," GENETICS, Vol 73, No 1, 1973, 125.
17. Gustafsson, A., and Dormling, I. "Dominance and Overdominance in Phytotron Analysis of Monohybrid Barley," HEREDITAS, Vol 70, No 2, 1972, 185.
[485-10,657]

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UDC: 575.1:581.167:633.11

VARIABILITY OF GENETIC PARAMETERS IN DIALLELE ANALYSIS OF QUANTITATIVE CHARACTERS OF SOFT SPRING WHEAT. REPORT 1: NUMBER OF SPIKELETS PER SPIKE

Moscow GENETIKA in Russian Vol 14, No 8, 1978 pp 1409-1422

[Article by R. A. Tsil'ke, O. T. Kachur and S. A. Sadykova, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 10 May 77, corrected copy received 15 Aug 77]

[Text] Introduction

The objective of modern breeding is to develop cultivars capable of maximum expression of genetic potential for crop productivity under specific natural and climatic conditions. The effectiveness of breeding programs is largely determined by knowledge of the nature of inheritance of characters related to plant productivity. However, expression and inheritance of quantitative characters are closely interrelated with mechanisms of expression of genetic information in ontogenesis. One of the important elements of this mechanism is capacity for competition, which is determined genetically and, at the same time, subject to the influence of the environment [1]. If we consider that expression of the genetic potential for productivity is related to intrapopulation competitiveness, which is affected by the nutrition area, we should create conditions close to those of industrial fields, at least in plant density, in the breeding plots. However, at the early breeding stages, when it is necessary to select genotypes with a set of economically valuable traits, which are characterized by strong variability in phenotypic expression, it is desirable to raise hybrid populations in lower density planting, which rules out or significantly attenuates intergenotypic competition. The advantage of stands with an enlarged area of plant nutrition is also that, in such a case, there is a significant increase in coefficient of seed reproduction and, for this reason, it becomes possible to make a more comprehensive and faster evaluation of the breeding material.

With the above in mind, we decided to study the distinctions of the genetic system of control of several quantitative characters of soft spring wheat as related to different plant densities and, on the basis of the experimental data, to consider some questions of selection of base material to be used in breeding programs, and of effectiveness of selection in segregating generations of hybrids.

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In this article, we report the results of experiments pertaining to the study of number of spikelets per spike. This character is closely related to spike productivity, and for this reason it is of importance to breeding.

Recent surveys of works dealing with the results of hybridological analysis of number of spikelets per spike revealed that this trait is characterized mainly by intermediate inheritance, with occasional expression of dominance [2, 3]. Unlike most other quantitative characters of wheat, the trait under study is relatively stable in its expression under different vegetation conditions. Diallele crosses can furnish the most complete information about genetic control of a quantitative character.

The principles of genetic analysis of the results of studies of diallele hybrids were expounded by Hull [4], Yates [5], Jinks [6, 7] and Hayman [8-10] on the basis of the classical works of Fisher et al. [11, 12] and Mather [13]. Works dealing with diallelic analysis have been published in our country [14, 15]. All of the studies involving the use of diallele analysis revealed that the number of spikelets is controlled mainly by genes with additive action and, in some cases, there is a dominant effect [2, 3]. However, it has not been determined how the genetic parameters in diallele analysis change when the nutrition areas vary when raising the plants.

Material and Methods

We used seven cultivars of soft spring wheat, which differ appreciably in economically valuable characters, as the parents. Table 1 lists brief information about the cultivars. The choice of the cultivars for our experiment was governed by the results of state testing thereof in the West Siberian region.

Hybrid seeds were obtained in 1971 from an irrigated plot of the institute. A special system of hybridization and growing the cultivars was developed in order to obtain at least 1000 seeds from each of 42 combinations. Coinciding stages of florescence of maternal and paternal parents were provided by sowing dates. The cultivars were crossed in accordance with a full diallele scheme, including intravarietal crosses. Some of the F_1 hybrid seeds were sown in the hothouse in the winter of 1971-1972 in order to obtain F_2 seeds. Parent cultivars, F_1 and F_2 hybrids were raised in the field in 1972 and 1973 in 2 experiments, which differed in plant density: experiment 1 (Exp-1), where the area of plant nutrition constituted 400 cm^2 (10×40) and experiment 2 (Exp-2), with a nutrition area of 40 cm^2 (2×20). The number of seeds sown per m^2 constituted 25 and 250, respectively. The experiments were conducted in 4-fold replications. The variants (cultivars and hybrids) were arranged at random in the blocks. The cultivars, F_1 and F_2 hybrids were raised in 1972 in Exp-1, and only cultivars and F_1 hybrids in Exp-2; in 1973, the cultivars, as well as F_1 and F_2 hybrids, were raised in both experiments. Sowing was performed on 15-16 May. The crops were dusted with vofatoks (metaphos) during the

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period between germination and "shooting" to control wheat flea beetles and "skrytostebel'nyye" [stem-boring?] pests.

Table 1. Characteristics of cultivars used in the experiment

Cultivar	Abbreviation used in this article	Origin (country or region)	Most valuable traits
Saratovskaya 29	S29	USSR, Povolzh'ye	High technological grain quality, drought resistance
Mil'turum 553	M553	USSR, West Siberia	Resistance to spring and summer drought
Novosibirskaya 67	N67	USSR, West Siberia	Resistance to lodging, responsiveness to water and fertilizers
Grecum 114	G114	USSR, Non-chernozem region	Resistance to lodging, large kernels
Pirotriaks 28	P28	USSR, North Kazakhstan	Drought resistance, high potential productivity
World Seeds 1877	W77	United States	Resistance to brown and stem rust, short stem
World Seeds 1812	W12	United States	Same as above

The meteorological conditions differed in the 2 years of the experiment: In 1972 there was 31 mm more precipitation in June and 18 mm more in August than the norm, and 13 mm less in July. Air temperature was 1.1° lower than the perennial mean in June, 1.9° lower in July and 1.5°C lower in August. The significant shortage of warmth with good supply of water created unfavorable conditions during formation [plumping] and maturation of the grain. Moreover, the torrential rains in August caused lodging of the long-stemmed cultivars and hybrids. In 1973, the mean monthly temperature was somewhat lower than the perennial mean in May, June and August, and 0.4°C higher than this mean in July. During the period of plant vegetation, there was 31 mm more rainfall than the norm. However, the brief drought in the first half of July had an adverse effect on formation of structural elements of the spike, particularly with the usual plant density.

The plants were gathered at the end of the yellow-ripe stage, then dried and their structural elements analyzed. We excluded from the analysis plants that presented a regional [marginal?] effect. The experimental data were submitted to variance analysis. The differences between variants

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were highly reliable ($P < 0.001$) in all cases. The differences between replications were also reliable. Reciprocal effects were reliable for some hybrid combinations, but negligible in value and for this reason we used the means for the character in reciprocals in our analysis. In this article we have adopted the following abbreviations: V_r --variance of series; W_r --covariance of series; \hat{D} --component of variability determined by additive gene action; \hat{F}_r --component reflecting dominant and additive effects in the series; $\bar{\hat{F}}_r$ --mean value of \hat{F}_r for all series in the diallele table; \hat{h}_1 and \hat{h}_2 --components reflecting positive and negative effects of genes; \hat{h}^2 --algebraic sum of dominant effects of heterozygous loci for all hybrids; \hat{E} --paratypical component of variability.

We tested homogeneity of W_r -- V_r to prove the validity of the hypothesis upon which diallele analysis is based [8]. In all cases, it was proven with high reliability that the requirements of material used in the experiment were met with respect to spikelets per spike. Diallele analysis was performed using a previously described method [16], and the obtained data were interpreted according to Hayman [8].

Experimental Section

Table 2 lists the mean values for the character in parents (\bar{x}) and several hybrids from each parent (\bar{x}_0). As we see, the cultivars used in the crosses differ appreciably in number of spikelets per spike, and vegetation conditions, as well as plant feeding area, have a significant effect on expression of the trait. In 1972, the difference between parent variants with the use of the larger nutrition area (Exp-1) constituted 6.6 and with the usual area (Exp-2) 6.1 spikelets. However, an average of 2 spikelets more was formed in Exp-1 than in Exp-2. In 1973, which was less favorable in water supply, the difference in Exp-1 constituted 7.4 spikelets and in Exp-2 3.9. It should be noted that, in 1973, on the average 2.4 fewer spikelets were formed in Exp-1 and 3.2 spikelets less in Exp-2 than in 1972. Thus, on the whole, there were fewer spikelets per spike in 1973 than in 1972, and fewer spikelets were formed, regardless of year, in the case of the usual nutrition area than with enlargement thereof. However, the cultivars reacted differently to these two factors: While the differences between cultivars were more marked in 1973 than 1972 with the use of the larger nutrition area (Exp-1), in the case of the ordinary area (Exp-2) they leveled off. This means that, regardless of environmental conditions, there is fuller expression of genetic potential in the case of sowing at a lower density than with the usual density of plant stands.

Comparative analysis of group means for parents and F_1 hybrids (\bar{X}) revealed that, on the whole, the trait is characterized by intermediate inheritance. However, with lower density planting, the group means for F_1 were lower in both 1972 and 1973 than for the parents, which is indicative of partial dominance in the direction of the parent with fewer spikelets per spike. In the case of high-density planting (Exp-2) the group means were the same for parents and F_1 hybrids in 1972, while the mean for F_1 was higher than

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the mean for the parents in 1973. If we compare the mean values of the trait for each parent to the mean values for hybrids involving the same parent, we shall see that the cultivars differ in degree and direction of dominance. The group means for F_2 were similar in value to the group means for F_1 .

Table 2. Number of spikelets per spike in parents (\bar{x}) and hybrids (\bar{x}_0)

Cultivar	1972						1973					
	Exp-1			Exp-2			Exp-1			Exp-2		
	P	F ₁	F ₂	P	F ₁	F ₂	P	F ₁	F ₂	P	F ₁	F ₂
W 12	14.9	16.7	17.0	13.6	15.2	12.2	13.6	13.5	11.4	12.8	12.9	
W 77	15.3	16.5	16.8	13.4	14.7	12.6	13.8	13.6	11.6	12.7	12.4	
S 29	16.7	17.1	17.4	14.9	15.8	14.2	14.8	14.7	12.2	13.1	12.9	
N 67	19.4	18.4	18.4	17.2	16.4	16.6	15.9	15.6	13.4	13.6	13.6	
G 114	20.3	18.8	19.0	17.9	17.1	18.4	16.4	16.2	14.6	14.0	14.0	
M 553	20.1	18.9	19.3	16.8	16.9	16.8	16.1	16.1	12.8	13.4	13.4	
P 28	21.5	19.6	20.0	19.5	17.6	19.6	17.0	17.1	15.3	14.3	14.3	
N	18.2	18.0	18.3	16.2	16.2	15.8	15.4	15.3	13.0	13.4	13.4	
with NCP P<0.05		0.72		0.28			0.80		0.40			

Table 3. Results of variance and covariance analysis

Parameter	1972			1973			
	Exp-1		Exp-2	Exp-1		Exp-2	
	F ₁	F ₂	F ₁	F ₁	F ₂	F ₁	F ₂
\hat{D}	6.35 ***	6.81 ***	5.22 ***	7.96 ***	7.96 ***	2.08 ***	2.07 ***
\hat{F}	-1.11 ***	-1.09 **	-0.57 ***	-1.48 ***	-1.71 ***	-0.07 *	-0.23 *
\hat{H}_1	0.40 **	0.40 *	0.30 *	0.59 ***	0.43 **	0.04 *	0.13 *
\hat{H}_2	0.33 **	0.42 *	0.27 *	0.58 ***	0.31 **	0.03 *	0.11 *
\hat{H}_3	0.12	0.06	0.03	0.36 ***	0.66 ***	0.29 ***	0.22 **
$(\hat{H}_1, \hat{H}_2)^{\frac{1}{2}}$	0.24	0.26	0.24	0.28	0.24	0.13	0.25
\hat{H}_2, \hat{H}_3	0.21	0.23	0.22	0.25	0.20	0.22	0.21
$(\hat{H}_1, \hat{H}_3)^{\frac{1}{2}} +$ $+ \hat{F}(\hat{H}_1, \hat{H}_3)^{\frac{1}{2}} -$ $- \hat{F}$	0.49	0.53	0.63	0.49	0.37	0.78	0.63
\hat{F}	0.10 **	0.14 **	0.07 ***	0.17 ***	0.17 ***	0.10 ***	0.11 ***
ρ	0.71	0.95	0.29	0.25	1.08	0.70	1.55

* P<0.05. ** P<0.01. *** P<0.001.

The results of variance and covariance analysis listed in Table 3 show that the trait is controlled in the material studied mainly by genes with additive action. Vegetation conditions and, particularly, plant feeding area have a substantial influence on genetic component \hat{D} , which reflects additive gene action. In all cases, the value of \hat{D} is highly reliable ($P<0.001$). While \hat{D} fluctuated insignificantly in different years in the case of low-density sowing (Exp-1), it was one-half the 1972 level in 1973 in the case of high-density sowing (Exp-2). This is related to the fact that there was smoothing of genotypic differences between cultivars

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in the experiment where there was the usual density of plant stands. Under these conditions, the genetic potential of each parent was not realized. Parameter \hat{F} , which reflects the direction of dominance as a whole for all hybrids, fluctuated significantly according to vegetation conditions, feeding area and generation studied. A minus sign for this parameter shows that, on the whole, there was expression in hybrids of dominance in the direction of the parent that formed fewer spikelets per spike. In 1972, the value of \hat{F} in Exp-1 was double the value in Exp-2. In 1973, the figures were -1.48 for F_1 and -1.71 for F_2 in Exp-1, -0.07 and -0.23 in Exp-2.

Parameters \hat{H}_1 and \hat{H}_2 are closely interrelated and reflect the contribution of genes with positive effects that increase the number of spikelets and those with negative ones that reduce the number of spikelets per spike. The values of these parameters were reliable in all cases. The correlation between these two parameters is reflected in index $H_2/4H_1$, which ranged from 0.20 to 0.25. This indicates that, in some cases, alleles with positive and negative effects were manifested in equal proportion (0.25) in some hybrids and unequal ones (0.20÷0.23) in others. The slight asymmetry of distribution of positive and negative alleles is also confirmed by the fact that $H_1 > H_2$ in all cases. It should only be mentioned that the differences between \hat{H}_1 and \hat{H}_2 were unreliable.

The parameter $(4\hat{D}\hat{H}_1)^{1/2} + \hat{F}/(4\hat{D}\hat{H}_1)^{1/2} - \hat{F}$ characterizes the overall proportion of dominant to recessive alleles in all parents. Since this index differed substantially from 1 (0.37-0.63) in all cases, it must be assumed that there is a disproportion between total number of dominant and recessive genes in the material studied.

Parameter $(\hat{H}_1/\hat{D})^{1/2}$, which characterizes the mean degree of dominance for all heterozygous loci, ranged from 0.13 to 0.28, which is indicative of partial dominance. This type of inheritance is also confirmed by the fact that all lines of regression of covariances W_r as functions of V_r pass above the starting point of the coordinates (Figures 1 and 2).

Analysis of the data in Table 3 shows that the genetic components of variability fluctuated over a rather wide range, depending on vegetation (year) conditions and area of plant feeding (experiment). A comparison of the parameters obtained from the results of evaluating F_1 and F_2 leads us to conclude that no significant differences in such indices as \hat{D} , \hat{H}_1 , \hat{H}_2 and proportion of genes with dominant and recessive effects, as well as genes with positive and negative action, are demonstrable with respect to number of spikelets per spike. However, the parameters \hat{D} , \hat{F} , \hat{H}_1 and \hat{H}_2 only give us an idea about the genetic system of control of the trait in the material as a whole, whereas for practical breeding purposes we need information about the specific cultivar to be used in crosses.

Table 4 lists the values of \hat{F}_r for each parent, which were obtained from the estimates of F_1 and F_2 hybrids. As a rule, this parameter is not calculated, and researchers limit themselves to the graphs of regression of

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W_r as a function of V_r . We believe that parameter \hat{F}_r supplements the information concerning the nature of inheritance of the trait for a specific parent.

Table 4. Results of estimation of \hat{F}_r

Cultivar	1972			1973			
	Exp=1		Exp=2	Exp=1		Exp=2	
	F_1	F_2	F_1	F_1	F_2	F_1	F_2
W12	-1.74***	-1.59***	-0.07	4.69***	0.08	-1.05***	-1.35***
W77	1.87***	-3.95***	1.25***	3.78***	1.79***	-0.02	0.63***
S29	-2.90***	-0.12	-1.59***	-2.01***	-1.88***	-0.15*	0.28**
N67	-0.73***	-1.68***	-2.14***	-2.40***	-1.85***	0.09	-0.50***
G114	-2.66***	0.07	-1.45***	-6.66***	-7.15***	-0.16*	-1.12***
M553	-1.40***	1.27**	1.17***	-2.50***	-0.63*	0.08	0.35*
P28	-0.58***	1.60***	-1.18***	-5.21***	-2.30***	0.76***	0.10*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

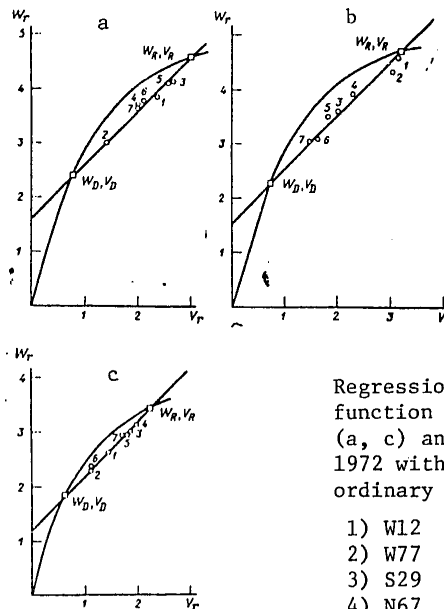


Figure 1.
Regression of covariances W_r as a function of variances V_r for F_1 (a, c) and F_2 (b) hybrids raised in 1972 with an enlarged (a, b) and ordinary (c) plant feeding area

- 1) W12 5) G114
- 2) W77 6) M553
- 3) S29 7) P28
- 4) N67

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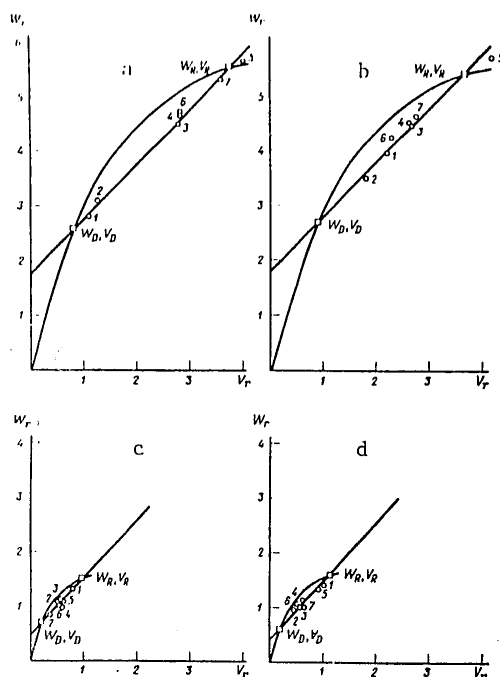


Figure 2.
Regression of covariances W_r as a function of variances V_r in F_1 (a, c) and F_2 (b, d) hybrids raised in 1973, with an enlarged (a, b) and ordinary (c, d) plant feeding area. Designations are the same as in Figure 1.

and in the rest there was expression of dominance of the parent with fewer spikelets per spike. In 1973, there was expression of dominance in the direction of the parent with more spikelets per spike in hybrids involving W12 and W77 in F_1 and W77 in F_2 in Exp-1, and expression of dominance of the one with fewer spikelets in the rest of the hybrids. In Exp-2, dominance was expressed in the direction of the parent with the greater number of spikelets in F_1 of hybrids derived from P28, F_2 of those derived from W77, S29, P28 and M553, while in other hybrids it was expressed in the direction of the parent with the lower number of spikelets. As can be seen in Table 4, there was no expression of stable level and direction of dominance in most hybrids. Relatively stable dominance in the direction of

Upon analyzing the data in Table 4, we were impressed, first of all, by the lability of parameter \hat{F}_r , the values of which fluctuated over a wide range, depending on weather, feeding area and generation studied. The value of \hat{F}_r was unreliable in 2 out of 21 cases in 1972 and 4 out of 28 in 1973. Consequently, there was expression in these hybrids of intermediate inheritance. In 1972, no dominance was expressed in F_1 of hybrids involving cultivars S29 and G114 (Exp-1) and F_2 hybrids involving W12 (Exp-1). In 1973, no dominance was expressed in F_1 hybrids derived from W12 in Exp-1 or in F_2 involving W77, N67 and M553 in Exp-2. Dominance was expressed in the direction of the parent with larger number of spikelets per spike in F_1 of hybrids involving W77 and F_2 involving M553 and P28 in the experiment with low density sowing (Exp-1) in 1972; in the rest of the hybrids it was expressed in the direction of the parent with the smaller number of spikelets. That same year, according to the results of evaluation of F_1 , with the usual density of plant stands (Exp-2), there was expression of dominance in the direction of the parent with the larger number of spikelets in hybrids derived from W77 and M553,

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the parent with more spikelets persisted only in hybrids involving short-stemmed cultivar W77. It should be noted that cultivar W77 itself is characterized by a low number of spikelets, as compared to most others used in the experiment. The value of \hat{F}_r fluctuated markedly, sometimes to the extent of a change in sign, in all hybrids involving the rest of the cultivars.

Table 5. Results of correlation and regression analysis

Coefficient of correlat.	1972				1973			
	Exp-1		Exp-2		Exp-1		Exp-2	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
r between \bar{x} & $W_r + V_r$	0,212	-0,917*	0,480	0,928**	0,691	-0,712	0,037	
r^2	0,045	0,841	0,230	0,861	0,477	0,507	0,004	
r' between V_r & W_r	0,973***	0,983***	0,994***	0,997***	0,981***	0,982***	0,980***	
b_{W_r/V_r}	0,893	0,907	0,967	0,980	0,906	0,920	0,855	

* $P < 0,05$. ** $P < 0,01$. *** $P < 0,001$.

Table 5 lists the results of correlation and regression analysis, which enable us to derive some conclusions concerning the links between the mean values for the character in parents (\bar{x}) and level of dominance ($W_r + V_r$), as well as between V_r and W_r . As we see, the coefficient of correlation between \bar{x} and $W_r + V_r$ is reliable only in two cases. A high and negative value for the coefficient of correlation ($r = -0.917$) indicates that, according to estimates of F_2 in 1972, in the experiment with larger feeding area (Exp-1), a positive effect in expression of the trait is related to the dominant action of genes and a negative one, to recessive action. The high and positive coefficient ($r = 0.928$) obtained on the basis of the results of estimating F_1 in 1973, in the variant with enlarged nutrition area, indicates that the positive effect in expression of the trait in F_1 hybrids is related to recessive genes and negative effect to dominant ones. All other cases, where the coefficients of correlation between \bar{x} and $W_r + V_r$ are unreliable, indicate that the relative contribution of dominant and recessive genes to development of the character in hybrids depends on vegetation conditions, nutrition area and generation studied. It should be noted that the coefficients of determination r^2 are significantly lower than 1, with the exception of the two cases discussed above, when the coefficients of correlation were close to 1. High values of coefficients of correlation (r') between V_r and W_r and of coefficients of regression (b) of W_r as a function of V_r indicate that, in all cases, the lines of regression do not deviate appreciably from the line of the single slope. This is additional proof of the fact that, for the character in question, all requirements of base material used in diallele analysis were met [8].

The plots of regression of W_r as a function of V_r (see Figures 1 and 2) rendered on the same scale illustrate not only the variability of values of W_r and V_r , but the relative nature of expression of dominant and recessive

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effects in hybrids. The order of the cultivars along the line of regression of W_r as a function of V_r reflects entirely the relative share of dominant and recessive parental alleles. While only one cultivar expressed dominance ($p \approx 75\%$) in 1972 with the enlarged plant feeding area (Exp-1) in 1972, according to the results of evaluation of F_1 (see Figure 1a) and others expressed varying degrees of recessiveness ($q \approx 50-75\%$), the cultivars were more or less uniformly distributed along the regression line according to the results of estimation of F_2 (see Figure 1b), and W77 presented a change in direction of dominance, as a result of which it was close to the point of maximum recessiveness ($q \approx 100\%$). With the usual feeding area (Exp-2), in 1972 there was expression of dominance ($p \approx 75\%$) in two cultivars (W77, M553), according to results of evaluation of F_1 (see Figure 1c), while the others were situated in the middle section of the line of regression ($p \approx 50\%$), there being no appreciable difference between cultivars and none of the parents was close to the point of maximum dominance ($p = 100\%$) or maximum recessiveness ($q = 100\%$). In 1973, according to the findings on F_1 (see Figure 2a), there was expression of virtually complete dominance ($p \approx 100\%$) in W77 and W12 and complete recessiveness ($q = 100\%$) in G114 and P28; the other cultivars did not differ appreciably from one another and were situated slightly above the middle point on the line of regression ($q \approx 50-75\%$). Under the same conditions, but with estimation of F_2 (see Figure 2b), only G114 retained complete recessiveness ($q = 100\%$), dominance diminished ($p \approx 75\%$) in two cultivars (W12, W77) and the rest of the cultivars were situated in the middle segment of the line of regression. In 1973, there was a drastic drop in values of variances and covariances in Exp-2 and, as noted above, value of \bar{F}_r (see Table 4), the differences between cultivars being insignificant (see Figure 2c and d).

Discussion

With reference to the results of analysis as a whole, we should call attention to the fact that, even with regard to such a relatively stable trait in its phenotypic expression as the number of spikelets per spike, high variability is demonstrable for all of the calculated parameters as a function of vegetation conditions (year), density of plant stands in the field (nutrition area) and generation studied (F_1 and F_2). On the one hand, there is confirmation of the conclusion [2, 3] that the character is controlled mainly by genes with additive action and, on the other hand, it has been very clearly shown that the genetic system of control of the trait is strongly modified by the environment. Analysis revealed that the nature of inheritance of the character in the material studied cannot be attributed to additive action of genes alone.

Proceeding from the elementary conceptions of genetics, in the case of intermediate inheritance of a quantitative character, the mean values for F_2 and F_1 should not deviate appreciably from the averaged value of the trait in the original parents ($\bar{x}_F = \bar{x}_{F_1} = \bar{x}_{F_2}$), since with such inheritance the recombination of genes as a result of segregation does not alter the mean value for F_2 in relation to F_1 , although there may be expression of

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considerable phenotypic variability of the trait in F_2 . Consequently, in the case of strict intermediate inheritance, genetic parameters of similar value should be obtained in diallele analysis on the basis of the results of evaluation of F_1 and F_2 . Indeed, no appreciable differences in the main parameters (\hat{D} , \hat{F} , \hat{H}_1 , \hat{H}_2) were demonstrated according to the results of analyzing F_1 and F_2 data (see Table 3). However, as shown by analysis of values of F_r and curves of regression of W_r as a function of V_r , significant differences were observed between F_1 and F_2 , which compel us to believe that recombination of genes that control the character leads to a significant shift of mean value of the trait for the F_2 population, as compared to F_1 . Typically enough, the mean values of F_1 in series (x_0) did not differ appreciable from the means for F_2 . In essence, differences between F_1 and F_2 were observed in some hybrids within series, which led to dissimilar values of W_r and V_r in assessing F_1 and F_2 hybrids. These differences were reflected in the order of location of the parents on the regression lines (see Figures 1 and 2). The position of the parents coincided according to the results of estimation of F_1 and F_2 in only 5 out of 21 cases. There was relatively similar order of parents in Exp-1 in 1973 according to F_1 and F_2 .

The differences between mean values for the trait in F_1 and F_2 , which occurred in some hybrid combinations, could be due to partial dominance, with which the mean for F_2 deviates from the mean for F_1 . But this differences could have been due to difference in competitiveness of genotypes in the segregating generation. Thus, when short-stemmed cultivars are crossed with long-stemmed ones, plants are formed in F_2 that differ markedly in height as a result of recombination of genes that control stem length. For this reason, these plants were exposed to dissimilar conditions in the course of ontogenesis, which affected expression of genetic information determining development of other traits, in particular, elements of spike structure. In view of these distinctions, it must be conceded that, even by analyzing traits controlled chiefly by genes with additive action, apparently we cannot obtain unequivocal information about genetic control of the character on the basis of estimation of F_1 and F_2 . From the results of studying F_2 , one can determine the parameters that characterize the genetic system of control as a whole for the set of parents used in the diallele cross. At the same time, the question arises as to whether the results of evaluation of F_2 are suitable for calculation of variances and covariances needed to describe individual parents. On the basis of the genetic patterns at the basis of diallele analysis, it is not expedient to use F_2 for evaluation of the genetic structure of individual parents.

We should discuss in greater detail the influence of vegetation conditions and feeding area on variability of genetic parameters in diallele analysis. These two environmental factors interact with one another closely, and for this reason they cannot be considered apart from one another. As shown by analysis, there was no appreciable difference between genetic parameters of plants raised in different years in the case of an enlarged feeding area, whereas with the usual feeding area, close to the size used in

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industry, these parameters were significantly lower under the less favorable conditions in 1973 than in the more favorable vegetation conditions in 1972. Thus, not only the parameters reflecting dominant effects, but those characterizing the additive action of genes fluctuate markedly, depending on ambient conditions and density of plant stands. The values of V_r and W_r are even more unstable; they reflect the action of the genes of each parent and, first of all, the genes that express dominance or recessiveness. According to the principles of diallele analysis, the lower the values of V_r and W_r , the higher the share of dominant alleles and, accordingly, the lower the share of recessive alleles and, conversely, the higher these values, the higher the share of recessive alleles and lower that of dominant alleles involved in expression of the character in the heterozygote.

The obtained data indicate that the relative share of dominant and recessive alleles involved in phenotypic expression of the trait fluctuates over a wide range, depending on the parents and environment. If we compare the order of arrangement of parents on the line of regression of W_r as a function of V_r , excluding the results for F_2 , we shall see that, in most cases, the order is not the same, either in different years or in different experiments. Such variability of expression of dominance is indicative of complex interaction between dominant and recessive alleles in homologous loci, depending on the genotypic environment and exogenous conditions during ontogenesis. The phenomenon of allelic gene interaction and, in particular, dominance is closely linked with the general problem of gene action in ontogenesis. Many aspects of this problem, at any rate in higher plants, have not yet been resolved.

Ontogenetic formation of the character under study is controlled by many genes. The expressiveness of these genes changes at different stages of ontogenesis, depending on many factors of the endogenous and exogenous environment that either stimulate or inhibit their action. Since each gene makes an insignificant contribution to expression of this trait, we should expect that the influence of the exogenous environment could have a relatively greater effect than any gene individually. Since the number of genes controlling a quantitative character is proportionate to the number of phenotypic classes, determination of the number or group of genes in expression of dominance yields values that are underestimated [17]. On the basis of this thesis and the fact that variability of genetic parameters was very high in the experiment, we did not define the number of genes controlling the trait in question.

In most works dealing with diallele analysis, there is discussion of experimental data obtained as a result of growing the material under the same conditions and with the same density of plant stands. The unequivocal parameters then obtained reflect expression of genetic information under concrete conditions. However, in order to solve practical problems related to forecasting effectiveness of selection in order to upgrade the character, such results are obviously inadequate.

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As shown by our findings, vegetation conditions and density of plant stands have such a strong influence on expression of the genetic system of control of the character in ontogenesis that it is difficult to obtain unequivocal solutions to problems of forecasting the results of breeding. Diallele analysis implies that the forecast of obtaining a genotype with all genes having a dominant or recessive effect in the set of parents studied can be made only if the coefficient of determination (r^2) between the mean values of the trait for the parents (\bar{x}) and level of dominance ($W_R + V_R$) is close to 1 [8]. In our experiment, this coefficient was close to 1 (0.861) only in 1973, in the experiment with low density sowing (Exp-1), according to evaluation of F_1 ; in all other cases, with the exception of the findings for F_2 , the coefficients were significantly smaller than 1. The estimates made according to Alsé and Johnson [16] revealed that the forecast of selection of the genotype with recessive genes that augment the number of spikelets per spike constitutes 18.6 spikelets. This is somewhat higher than for cultivar G114 (18.4 spikelets), but lower than for P28, which formed the largest number of spikelets per spike (19.4) under these conditions. On the line of regression of W_R as a function of V_R (see Figure 2a), these two cultivars are close to the point of maximum recessiveness acting in the direction of increase in number of spikelets. Consequently, in the early segregant generations of hybrids derived from cultivars G114 and P28, some recessive alleles in heterozygotes were overlapped by dominant alleles lowering the phenotypic expression of the trait. Since the level and direction of dominance change as a function of ambient conditions and plant density, it is not possible to reliably predict the genetic effect of selection in segregating generations according to genes expressing dominance or recessiveness.

It is simpler to predict the improvement of the trait under study by breeding because it is controlled mainly by genes with additive action, which is reflected relatively completely in phenotypic expression in parents. In breeding programs used to augment spike productivity by increasing the number of spikelets for the conditions prevailing in Siberia, it is recommended that cultivars G114 and P28 be used, as they are characterized by high expressiveness of this trait under different vegetation conditions and with different density of plant stands. However, it should be noted that fullest expression of the genetic potential for this trait was observed in the case of low density sowing; for this reason, selection should be pursued in fields with an enlarged and uniform area of plant feeding. Since genetic variability of the character is related mainly to the additive action of genes, it is recommended that selection be started in early segregating generations (F_2 - F_3). But it must be borne in mind that there may be expression of partial dominance in the direction of attenuation of phenotypic expression of the trait in hybrids involving G114 and P28, in segregating generations, in genotypes that are heterozygous for the loci that control the number of spikelets; therefore, selection would also be effective in later generations (F_4 - F_5) for some breeding lines. It must be noted that the short-stemmed American cultivars W77 and W12 are not suitable for improvement of the character under study in developing cultivars for

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local conditions. Siberian cultivar M553, widely zoned S29 and the new radiation cultivar N67 can be used in breeding programs, but will be less effective than G114 and P28. Of course, we are referring here only to the number of spikelets per spike.

Our study confirms the conclusion of Gilbert, who made a critical scrutiny of the effectiveness of diallele analysis for practical purposes, to the effect that such analysis makes it possible to refine the breeding process, but does not replace the creative intuition of the breeder. At the same time, it is quite obvious that diallele analysis is, for the time being, one of the most effective methods of studying the genetic system of control of quantitative characters.

Conclusions

Diallele analysis revealed that there is high variability of genetic parameters related to number of spikelets per spike, depending on vegetation conditions (year), density of plant stands (area of nutrition) and generation studied (F_1 and F_2). It was demonstrated that this character is controlled chiefly by genes with additive action; however, genes with dominant effects also make a significant contribution to the genetic system of control of the trait in hybrids. The cultivars used in the experiment differ appreciably in nature of allelic interaction of genes that determine development of spikelets in the spike.

Component \hat{D} , which reflects the additive action of genes, showed less fluctuation in different years in the case of low density sowing than usual sowing.

On the average, all hybrids expressed partial dominance in the direction of the parent with fewer spikelets per spike; however, the cultivars differed substantially in component \hat{F}_r , which reflects the direction of dominance for the group of hybrids referable to each cultivar.

The relative contribution of dominant and recessive alleles, as well as contribution of genes with positive and negative effects, to phenotypic expression of the character fluctuated significantly, depending on vegetation conditions and plant feeding area.

There are 5 tables and 2 figures; bibliography lists 18 items.

BIBLIOGRAPHY

1. Kan-Ikhi-Sakay "Competitiveness of Plants, Its Heritability and Some Related Problems," in "Mekhanizmy biologicheskoy konkurentsii" [Mechanisms of Biological Competition], Moscow, Mir, 1964, p 309.

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2. Walton, O. D. "Quantitative Inheritance of Yield and Associated Factors in Spring Wheat," EUPHYTICA, Vol 21, No 3, 1972, 553.
3. Halloran, G. M. "Genetic Analysis of Yield in Wheat," Z. PFLANZENZUCHT, Vol 74, No 4, 1975, 298.
4. Hull, F. H. "Regression Analysis of Yields of Hybrid Corn and Inbred Parent Lines," "Maize Genetics Coop. Newsletter," No 19, 1945, 21.
5. Yates, F. "Analysis of Data From All Possible Reciprocal Crosses Between a Set of Parental Lines," J. HEREDITY, Vol 1, 1947, 287.
6. Jinks, J. L. "The Analysis of Continuous Variation in a Diallele Cross of Nicotiana Rustica Varieties," GENETICS, Vol 39, No 6, 1954, 767.
7. Idem, "A Survey of the Genetical Basis of Heterosis in a Variety of Diallele Crosses," Ibid, Vol 9, 1955, 229.
8. Hayman, B. I. "The Theory and Analysis of Diallele Crosses," GENETICS, Vol 39, No 6, 1954, 789.
9. Idem, "The Analysis of Variance of Diallele Tables," BIOMETRICS, Vol 10, 1954, 235.
10. Idem, "The Theory and Analysis of Diallele Crosses," GENETICS, Vol 43, No 1, 1958, 63.
11. Fisher, R. A. "The Correlation Between Relatives on the Supposition of Mendelian Inheritance," TRANS. ROY. SOC. EDINBURGH, Vol 52, 1918, 399.
12. Fisher, R. A.; Immer, F. R.; and Tedin, O. "The Genetical Interpretation of Statistics of the Third Degree in the Study of Quantitative Inheritance," GENETICS, Vol 17, 1932, 107.
13. Mather, K. "Biometrical Genetics," Lond, Methuen and Co., 1949, pp 52, 162.
14. Fedin, M. A., and Silis, D. Ya. "A Method of Analysis of Quantitative Characters of Plants by Means of Diallele Crosses," in "Geneticheskii analiz kolichestvennykh priznakov s pomoshch'yu matematiko-statisticheskikh metodov" [Genetic Analysis of Quantitative Characters Using Statistical and Mathematical Methods], Moscow, All-Union Scientific Research Institute of Technical and Economic Agricultural Information, 1973, pp 82, 114.

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15. Turbin, N. V.; Khotyleva, L. V.; and Tarutina, L. A. "Diallele Analysis in Plant Breeding," Minsk, Nauka i Tekhnika [Science and Technology], 1974, p 184.
16. Aksel, R., and Johnson, L. P. V. "Analysis of a Diallele Cross: a Worked Example," ADVANCING FRONTIERS OF PLANT SCIENCE, Vol 2, No 16, 1963, 37.
17. Gershkovich, I. "Genetika" [Genetics], Moscow, Nauka, 1968, p 698.
18. Gilbert, N. E. G. "Diallele Cross in Plant Breeding," J. HEREDITY, Vol 12, 1958, 477.
[485-10,657]

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COMBINING ABILITY OF SOFT SPRING WHEAT CULTIVARS FOR KERNEL SIZE UNDER
THE CONDITIONS OF WEST SIBERIA

Moscow DOKLADY VASKhNIL in Russian No 11, 1978 pp 1-3

[Article by R. A. Tsil'ke, candidate of agricultural Sciences, and O. T. Kachur, Siberian Scientific Research Institute of Agriculture, submitted 9 Mar 78, presented by A. V. Pukhal'skiy, academician of VASKhNIL (All-Union Order of Lenin Academy of Agricultural Sciences imeni V. I. Lenin) on 10 Mar 78]

[Text] In the last few years, there has been considerable refinement in Siberia of the technology for growing wheat and this, in turn, has imposed new requirements of cultivars. The diversity of soil and climate, rigor and variability thereof pose problems of exceptional difficulty to breeding. The effectiveness of breeding programs based on gene recombination depends largely on the combining ability of the base material used in hybridization. Special mathematical methods have been developed for analysis of general (GCA) and specific (SCA) combining ability of genotypes according to the results of evaluation of hybrid offspring (F_1 and F_2) obtained from systemic crosses [2]. It is known that expression of the genetic potential for varietal productivity depends on environmental factors and, in particular, area of plant feeding [1].

Our objective was to study the nature of expression of combining ability of seven soft spring wheat cultivars as related to vegetation conditions (year) and area of plant nutrition (experiments). In this article, we report the results of evaluating the cultivars according to grain size. The worldwide pool of genes of hexaploid wheat is characterized by significant diversity of kernel size, the index of which is the weight per 1000 kernels. It has been shown in several works that this character is controlled mainly by genes with additive action; however, dominant and overdominant effects also have an appreciable influence on development of traits in hybrids [3-6].

The cultivars used in the experiment were crossed following a full diallele scheme. The parents, F_1 and F_2 hybrids were raised in the field in 1972 and 1973, in two experiments differing in plant feeding area: experiment 1

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Table 1. Weight per 1000 kernels for cultivars, F₁ and F₂ hybrids (g)

Variety	1972						1973					
	exp-1			exp-2			exp-1			exp-2		
	P (X)	F ₁ (u/m)	F ₂ (u/m)	P (X)	F ₁ (u/m)	F ₂ (u/m)	P (X)	F ₁ (u/m)	F ₂ (u/m)	P (X)	F ₁ (u/m)	F ₂ (u/m)
World Seeds 1877	36.6	38.2+44.7	33.6+40.3	29.5	36.2+41.4	—	35.0	36.6+45.6	36.6+38.0	30.0	34.5+41.2	32.1+35.0
World Seeds 1812	36.7	40.8+47.3	34.7+45.9	31.4	36.2+41.4	—	33.7	38.4+46.2	35.9+41.0	32.9	37.2+42.1	34.5+37.9
World Seeds 283	34.0	33.9+45.5	31.0+41.0	37.9	38.0+46.6	—	36.4	37.5+42.5	34.7+44.2	33.3	34.5+42.1	32.1+40.4
Novosibirskaya 67	26.6	33.9+45.3	31.0+40.5	35.1	37.0+45.9	—	38.9	36.6+47.6	37.1+45.6	37.7	35.4+43.4	33.0+40.6
Saratovskaya 29	40.2	40.6+48.8	37.8+47.1	38.9	36.4+47.1	—	42.1	39.2+50.8	37.7+47.6	38.5	36.4+45.2	34.4+43.4
Grecum 114	43.5	41.4+50.0	38.3+46.5	41.5	38.0+47.4	—	42.0	39.2+48.6	38.0+49.3	39.2	37.3+45.5	34.1+41.3
(X)	39.0	44.7+50.0	40.3+47.5	49.2	39.4+47.4	—	49.1	45.6+50.8	37.2+49.3	43.7	41.2+45.2	34.0+41.3
	38.2	42.7	39.4	38.6	40.9	—	39.2	42.3	40.4	36.5	39.5	37.2

[exp-1], low density sowing with 10×40 cm feeding area (400 cm²); experiment 2 [exp-2], ordinary sowing density with nutrition area of 2×20 cm (40 cm²). When scaled to 1 m², the number of seeds planted was 25 in exp-1 and 250 in exp-2. The meteorological conditions were not the same in the 2 years. The vegetation conditions in 1972 were characterized by a shortage of warmth, but good precipitation, whereas 1973 was relatively favorable for plant development with regard to temperature and water.

The results of variance analysis revealed that the differences between cultivars (P) and hybrids (F₁ and F₂) were highly reliable (P<0.001).

Analysis revealed that the variances were significantly greater for GCA than SCA. This shows that genes with additive action make a substantial contribution to the genetic system of control of the trait. In the case of low density sowing (exp-1), the differences between genotypes were more distinct according to GCA. Although the SCA variances were strongly inferior to SCA they still indicated that genes with allelic and nonallelic interaction had a considerable influence on development of the character in the hybrids.

The data listed in Table 1 indicate that the base cultivars differed appreciably in nature of expression of the character, and the means were relatively stable in different years and experiments. However, as shown by the group means (X), the character was expressed more stably in the hybrids as a whole than the cultivars. Moreover, the hybrids formed larger kernels than the cultivars, which is indicative of expression of dominant and overdominant effects. As a rule, the weight per 1000 kernels dropped markedly in F₂, as compared to F₁. This indicates that the heterosis effect is related mainly to heterozygosity of the loci controlling the trait in question. Regardless of year and plant feeding area, Grecum 114 and hybrids derived from it formed the largest kernels.

As can be seen in Table 2, the effects of GCA fluctuated significantly, depending on vegetation

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conditions, plant feeding area and the hybrid generation studied; however, the sequence (ranks) of the cultivars is relatively stable according to estimates of GCA. Positive effects of GCA were obtained for cultivars Grecum 114, Novosibirskaya 67 and Saratovskaya 29. It should be noted that Grecum 114 was several times superior to the other two cultivars in magnitude of GCA effects.

Table 2. Effects of GCA of cultivars on weight per 1000 kernels (g)

Cultivar	1972						1973					
	exp-1			exp-2			exp-1			exp-2		
	F ₁		F ₂	F ₁		F ₂	F ₁		F ₂	F ₁		F ₂
	\bar{g}_1	rank	\bar{g}_2	rank	\bar{g}_1	rank	\bar{g}_1	rank	\bar{g}_2	rank	\bar{g}_1	rank
World Seeds 1877	-1.66	3	-2.04	3	-3.96	1	-3.13	1	-4.17	1	-2.25	2
" " 1812	0.41	4	-0.19	4	-2.42	2	-1.76	2	-2.32	2	-1.05	3
Pirotriaks 28	-2.76	1	-3.11	2	-0.21	3	-2.05	3	-1.49	3	-2.46	1
Mil'turum 553	-2.47	2	-3.24	1	-0.10	4	-0.98	4	-0.05	4	-0.38	4
Novosibirskaya 67	1.21	6	1.76	5	0.58	5	1.43	5	1.65	5	-0.02	5
Saratovskaya 29	0.59	5	2.85	8	1.61	6	0.32	6	1.83	6	1.34	6
Grecum 114	4.57	7	4.86	7	4.50	7	6.18	7	4.54	7	4.82	7
Standard error($\bar{g}_1 - \bar{g}_2$)	0.33	—	0.55	—	0.13	—	0.31	—	0.36	—	0.32	—

Although the nature of expression of the character in parents reflects, to some extent, the relative value of the genotype, only evaluation of hybrid offspring yields objective information about the genetic potential of a cultivar. This can be well seen in cultivars Novosibirskaya 67 and Saratovskaya 29, which showed similar results with regard to weight per 1000 kernels, but differed appreciably in general combining ability.

This study indicated that overall combining ability of cultivars, according to weight per 1000 kernels, was expressed relatively stably under different vegetation conditions and different density of plant stands. It was established that the new cultivar, Grecum 114, has the highest and relatively stable GCA, and it is a unique source of genes that can be used effectively in breeding programs as a donor for kernel size. In view of the fact that kernel size is controlled mainly by genes with additive action, selection for this character will be effective in early segregating generations (F₂ and F₃). It is expected that selection will be the most effective among the hybrid combinations Saratovskaya 29 × Grecum 114, Novosibirskaya 67 × Grecum 114, in which considerable transgressive segregation is expressed for the parameters that determine kernel size.

BIBLIOGRAPHY

1. Sinyagin, I. I. "Plant Feeding Areas," Moscow, Rossel'khozizdat, 3d edition, 1975.
2. Griffing, J. B. AUSTRAL. J. BIOL. SCI., No 9, 1956.

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3. Halloran, G. M. Z. PFLANZENZUCHT., Vol 74, No 4, 1975, 298.
4. Hsu, P., and Walton, P. D. CAN. J. GENET. AND CYTOL., Vol 12, No 4, 1970, 738.
5. Idem, EUPHYTICA, Vol 19, No 1, 1970, 54.
6. Walton, P. D. Ibid, Vol 21, No 3, 1972, 553.
[485-10,657]

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VARIABILITY OF GENETIC PARAMETERS IN DIALLELE ANALYSIS OF QUANTITATIVE CHARACTERS OF SOFT SPRING WHEAT. REPORT 2: STEM LENGTH

Moscow GENETIKA in Russian Vol 15, No 2, 1979 pp 273-285

[Article by R. A. Tsil'ke, O. T. Kachur and S. A. Sadykova, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 13 Oct 77]

[Text] Diallele analysis was made of seven cultivars of soft spring wheat according to stem length. It was shown that the genetic parameters vary significantly, depending on vegetation conditions (year), area of plant feeding and the hybrid generation studied. This character is controlled by an additive-dominant genetic system. The interaction that occurs between the genotype and environment has a strong influence on the results of analysis. Variability of the genetic parameters makes it difficult to predict the effectiveness of breeding for this trait.

Plant height plays a substantial role in resistance to lodging. In order to implement the practical tasks of developing cultivars with a specific plant height one must have information about the genetic system of control of stem formation under specific natural and climate conditions. Some of the questions related to the problem of developing lodging-resistant cultivars of soft spring wheat in the extremely continental climate of Siberia were discussed previously [1].

The studies conducted in different climates and of different base material revealed that stem length, as the main component of overall plant height, is characterized by a complex genetic control system, including genes with different types of action and interaction, and they differ significantly in phenotypic effect on expression of the character [2-26]. In some forms of wheat stem length is controlled by several genes, each of which is characterized by a strong phenotypic effect, and in others it is controlled by many genes expressing mild effects.

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Extensive use is made of short-stemmed forms in modern breeding programs; unlike long-stemmed ones, the former are characterized by a specific genetic system of control of the trait in question. When short-stemmed cultivars are crosses with long-stemmed ones, a wide phenotypic spectrum of plant height appears in segregating generations, and this poses a number of problems with respect to selection of elite plants and evaluation of breeding lines. In the course of ontogenesis, plants that differ appreciably in height are exposed to different conditions, with regard to some environmental factors, and this affects expression of genetic information that determines development of characters that are directly and indirectly related to plant productivity [2, 3]. If we also consider that expression of the genetic potential of genotype productivity depends on the vegetation conditions in the course of ontogenesis and area of plant feeding, we can understand the difficulties that arise in selecting and evaluating breeding material. Consequently, when determining the effectiveness of selection for stem length in segregating generations, we also solve breeding problems related to expression of genetic potential for varietal productivity. In spite of the urgency of developing cultivars for different geographic and climatic regions of the country that would be resistant to lodging, very little information has been accumulated to date concerning genetic control of formation of a stem of a specific length and its relation to development of other economically valuable characters under different plant-raising conditions [27-28].

In this article, we report the results of diallele analysis of stem length in soft spring wheat as related to vegetation conditions (years), area of plant nutrition (experiments) and generation studied (F_1 and F_2).

Material and Methods

The following cultivars were included in diallele analysis: Saratovskaya 29 (S29), Mil'turum 553 (M553), Novosibirskaya 67 (N67), Grecum 114 (G114), Pirotrix 28 (P28), World Seeds 1877 (W77) and World Seeds 1812 (W12). These cultivars differ substantially, not only in stem length and resistance to lodging, but in the set of economically valuable characters. The short-stemmed American cultivars W77 and W12, and medium-stemmed Soviet cultivars N67 and G114 are characterized by rather high resistance to lodging under the conditions of West Siberia. Medium-stemmed S29 and long-stemmed M553 and P28 are not resistant to lodging.

The cultivars, F_1 and F_2 hybrids were raised in the field in 1972 and 1973 in two experiments differing in area of plant feeding: experiment 1 (exp-1) with low-density sowing and feeding area of 10×40 cm (400 cm^2) and experiment 2 (exp-2), ordinary sowing pattern with feeding area of 2×20 cm (40 cm^2). When scaled to 1 m^2 , the number of germinating seeds planted constituted 25 in exp-1 and 250 in exp-2. The methods used in the experiments, characteristics of initial material and data pertaining to meteorological factors were described in our previous report [29].

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Experimental Section

Table 1 lists the mean values for the character in parents (\bar{x}) and means for hybrids derived from each parent (\bar{x}_0). As we see, the cultivars used in the experiment differed appreciably in stem length. They can be arbitrarily divided into 3 groups: short-stemmed (W12, W77), medium (S29, N67, G114) and long-stemmed (M553 and P28). Within each group, there was also a difference in expression of the trait in most cases. The American cultivars W12 and W77 formed a stem that was almost one-half the length of the Siberian M553 and P28. Of the medium-height cultivars, G114 formed the shortest stem. In 1972, this cultivar had a stem that was 12.5 cm shorter in the case of low-density stands (exp-1) and 5.9 cm shorter in the usual stands (exp-2); the figures for 1973 were 10.0 and 4.9 cm shorter, respectively, than in S29.

Table 1. Stem length in parents (\bar{x}) and hybrids (\bar{x}_0), cm

Culti- var	1972						1973					
	exp-1			exp-2			exp-1			exp-2		
	P	F ₁	F ₂	P	F ₁	F ₂	P	F ₁	F ₂	P	F ₁	F ₂
W12	53.4	78.3	76.4	57.7	81.9	49.4	74.9	71.5	56.7	84.7	82.8	82.8
W77	60.1	78.4	75.1	61.9	82.2	54.3	77.4	74.5	65.2	85.8	82.4	82.4
S29	97.7	91.4	89.7	96.1	95.0	103.6	97.0	94.0	103.0	101.5	99.5	99.5
N67	89.3	91.2	89.0	97.6	96.1	100.2	98.6	93.4	101.5	101.4	100.0	100.0
G114	85.2	89.6	86.4	100.2	96.5	96.6	97.3	94.1	98.1	101.7	98.8	98.8
M553	104.9	91.8	95.4	104.1	98.0	118.7	104.0	101.2	117.8	107.2	106.0	106.0
P28	101.3	97.0	95.0	110.6	99.2	109.4	103.1	101.0	118.0	107.1	105.5	105.5
X	84.6	88.7	86.8	88.4	92.7	89.4	93.2	90.0	94.3	98.5	96.4	96.4
HCP with P<0.05		3.98		1.58		2.34			1.77			

We were impressed by the fact that, although stem length varied, depending on vegetation conditions and plant feeding area, the fluctuations were not as significant as for number of spikelets per spike [29]. In 1973, the cultivars formed a longer stem than in 1972; and they formed a longer stem in the case of the usual sowing density than low density. Typically enough, the opposite was observed for number of spikelets: the cultivars formed more spikelets in 1972 than in 1973, and more with low-density sowing than the usual spacing. The negligible differences between group means for parents and F₁ hybrids (X) indicate that in the hybrids as a whole there was expression of intermediate inheritance; but, at the same time, the observed differences are still indicative of expression of dominant effects. The means for hybrids (\bar{x}_0) involving short-stemmed W77 and W12 were lower in all cases than the group means for the parents (\bar{x}), whereas they were higher for the hybrids involving medium- and long-stemmed S29, N67, G114, P28 and M553. The means for F₂ (\bar{x}_0) were lower in most hybrids than for F₁, which is also indicative of expression of dominant effects.

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Table 2. Results of variance and covariance analysis

Parameter	1972			1973			
	exp-1		exp-2	exp-1		exp-2	
	F_1	F_2	F_1	F_1	F_2	F_1	F_2
\hat{D}	402.82 ***	400.77 ***	418.39 ***	726.15 ***	724.39 ***	579.46 ***	579.71 ***
\hat{F}	88.38 ***	13.65 **	86.60 ***	-59.70 ***	-68.03 ***	54.99 ***	11.58 ***
\hat{H}_1	19.55 ***	10.76 **	55.54 ***	27.55 ***	23.67 ***	7.86 ***	0.01
\hat{H}_2	13.42 **	7.86 *	47.38 ***	20.11 **	16.03 **	7.25 ***	-0.58
\hat{h}^2	47.60 ***	10.16 ***	53.18 ***	36.48 ***	-4.14	47.47 ***	10.20 ***
$(\hat{H}_1/\hat{D})\%$	0.22	0.16	0.36	0.19	0.18	0.12	...
\hat{H}_2/\hat{H}_1	0.17	0.18	0.21	0.18	0.17	0.23	...
$(4\hat{D}\hat{H}_1)\% + \hat{F}$	2.28	1.23	1.79	0.85	0.59	2.37	...
$(4\hat{D}\hat{H}_1)\% - \hat{F}$	6.78 **	8.83 ***	4.98	8.20 *	9.95 ***	5.54 ***	5.30 ***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; — not calculated due to unreliability of one of the initial parameters.

As shown by the data in Table 2, in the material studied genes with additive action made the most substantial contribution to the genetic system of control of the character. Component \hat{D} , which reflects variability due to additive gene action, fluctuated over a rather wide range, depending on the year and density of plant stands. In 1972, the value of \hat{D} was higher in the case of usual spacing (exp-2) and this was true in 1973 in the case of low-density sowing (exp-1). On the whole, however, the values for component \hat{D} were considerably higher in 1973 than 1972, particularly in the case of larger plant feeding area (exp-1).

In addition to the additive action, dominant effects also make a significant contribution to the genetic system of control of the trait. The values of component \hat{F} , which reflects the direction of dominance as a whole for all hybrids, were reliable in different years, experiments and generations. It should be noted that the values of \hat{F} were positive in both experiments in 1972 and in exp-2 in 1973, and they were negative in exp-1 in 1973. These findings indicate that vegetation conditions and plant feeding area have a strong influence on the nature of allelic gene interaction in expression of the trait in hybrids, and these two environmental factors interact closely with one another and the genotype. This is apparent from the fact that, while the values of \hat{F} were considerably higher (86.60) in the case of usual plant spacing (exp-2) in 1972 than 1973 (54.99) and they were characterized by a positive sign, with low-density sowing the direction of dominance changed from positive in 1972 (69.38) to negative in 1973 (-59.70). We were impressed by the fact that, with evaluation of F_2 hybrids the values of \hat{F} were several times lower than in evaluation of F_1 . In view of recombination of genes controlling development of the stem, the mean for the segregant F_2 generation deviated from the mean for F_1 , which in turn affected the results of variance and

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covariance analysis. Parameters \hat{H}_1 and \hat{H}_2 were reliable in most cases, and they were higher in F_1 hybrids than F_2 . Moreover, in all cases, $\hat{H}_1 > \hat{H}_2$, which indicates an uneven proportion of genes with positive and negative effects in the material examined. This was also confirmed by the fact that parameter $\hat{H}_2/4\hat{H}_1$ deviated from the 0.25 level, ranging from 0.17 to 0.23, the deviations being more substantial with low-density sowing (exp-1) than usual density (exp-2).

The index of mean dominance $(\hat{H}_1/\hat{D})^{1/2}$ ranged from 0.12 to 0.36, which was indicative of the modifying effect of the environment on nature of expression of dominant effects. According to the results of evaluation of F_1 hybrids with the usual sowing density in 1972 and 1973, and low-density sowing in 1972, index $(4\hat{D}\hat{H}_1)^{1/2} + \hat{F}/(4\hat{D}\hat{H}_1)^{1/2} - \hat{F}$ was significantly greater than 1 (1.79, 2.37 and 2.28, respectively). This indicates that there was prevalence of genes with dominant effects in the material studied. However, this conclusion is not corroborated by the findings for F_1 hybrids in the case of low-density sowing in 1973, when the index is < 1 (0.65).

Table 3. Values of parameter \hat{F}_R

Parent	1972			1973			
	exp-1		exp-2	exp-1		exp-2	
	F_1	F_2	F_1	F_1	F_2	F_1	F_2
W12	-118.36 ***	-177.80 ***	-152.90 ***	64.50 ***	177.66 ***	-126.16 ***	-144.01 ***
W77	35.70 **	-81.02 ***	-117.07 ***	54.15 ***	86.74 ***	43.40 ***	62.91 ***
S29	-13.66 **	-45.27 ***	105.65 ***	28.02 *	-49.65 **	128.22 ***	66.87 ***
N67	145.89 ***	-26.32 **	98.84 ***	-92.30 ***	-280.35 ***	154.84 ***	64.21 ***
G114	135.90 ***	117.85 ***	111.82 ***	-216.98 ***	-187.00 ***	57.28 ***	-18.45 ***
M553	134.20 ***	185.65 ***	397.72 ***	-171.89 ***	-133.92 ***	86.33 ***	65.00 ***
P28	168.41 ***	102.46 ***	162.09 ***	-81.41 ***	-89.72 ***	60.66 ***	-15.48 ***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

With respect to analysis of the data in Table 3, it should be noted that the values of parameter \hat{F}_R , which reflects the relative contribution of genes with additive and dominant action to development of the trait in the group of hybrids derived from each parent, fluctuated over a rather wide range, depending on vegetation conditions, feeding area and generation studied. According to the results of evaluation of F_1 hybrids derived from short-stemmed W12, parameter \hat{F}_R was characterized by a negative value in both experiments in 1972 and exp-2 in 1973; it was positive in exp-1 in 1973. Different results were obtained when we evaluated F_1 hybrids derived from the other short-stemmed cultivar, W77: parameter \hat{F}_R was negative only in exp-2 in 1973, and it was positive in all other cases. According to the results obtained for F_1 hybrids involving N67, G114, M553 and P28, parameter \hat{F}_R was characterized by a positive sign in 1972 and negative in 1973 in the case of low-density sowing, whereas with the usual sowing density it was positive in both 1972 and 1973. Cultivar S29 differed in nature of inheritance of stem length from the other varieties in that the values of \hat{F}_R were significantly lower than for other cultivars in both experiments of 1972 and in exp-1 in 1973. It is

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important to mention that the values of \hat{F}_R from the results of evaluation of F_1 usually differed significantly from the results for F_2 .

The graphs of regression of W_R as a function of V_R (see Figures 1-3) yield the most complete information about manifestation of dominant and recessive effects. First of all, we should indicate that the lines of regression are situated considerably higher than the start of the coordinates on all curves. This confirms the fact that, on the whole, there is expression of partial dominance of stem length in hybrids.

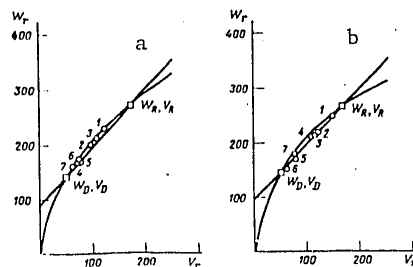


Figure 1.

Graphs of regression of W_R as a function of V_R , F_1 (a), F_2 (b), exp-1, 1972

- | | | |
|--------|---------|---------|
| 1) W12 | 4) N67 | 6) M553 |
| 2) W77 | 5) G114 | 7) P28 |
| 3) S29 | | |

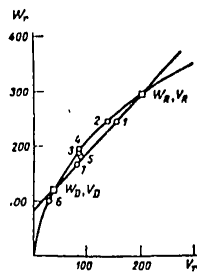


Figure 2.

Curves of regression of W_R as a function of V_R , F_1 , exp-1, 1972

Designations are the same as in Figure 1.

In 1972, in the variant with low-density sowing (exp-1), according to evaluation of F_1 (see Figure 1a), cultivars N67, G114, M553 and P28 expressed dominance ($p \approx 75\%$), while W12 presented recessiveness ($q \approx 50-75\%$). W77 and S29 were situated in the middle section of the line of regression, which is indicative of absence of appreciable dominant or recessive effects. According to results of estimates for F_2 (see Figure 1b), M553 was close to the point of maximum dominance on the line of regression ($p \approx 100\%$), while W12 was close to the one of maximum recessiveness ($q \approx 100\%$). G114 and P28 expressed dominance ($p \approx 75\%$), while W77, S29 and N67 showed recessiveness ($q \approx 50-75\%$). In the case of the usual sowing density (exp-2), according to results of evaluation of F_1 (see Figure 2), G114, S29, N67, P28 expressed dominance ($p \approx 50-75\%$), W12 and W77 recessiveness ($q \approx 75\%$), while M553 expressed maximum dominance ($p = 100\%$).

In 1973, there was an appreciable change in order of cultivars on the line of regression, as compared to 1972. With low-density sowing, according to results for F_1 (see Figure 3a), G114, N67, M553 and P28 expressed recessiveness ($q \approx 50-75\%$), while W12 presented dominance. W77 and S29

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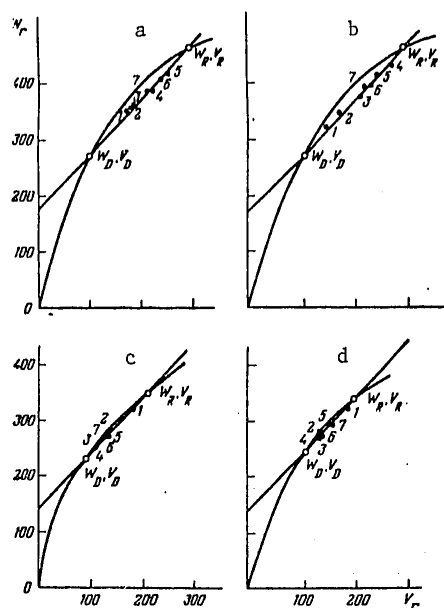


Figure 3.
Curves of regression of W_R as a function of V_R in 1973. Designations are the same as in Figure 1.

- a) F_1 , exp-1 c) F_1 , exp-2
b) F_2 , exp-1 d) F_2 , exp-2

were situated in the middle section of the line of regression. Upon evaluation of F_2 (see Figure 3b), the order of the cultivars on the line of regression did not change appreciably, as compared to F_1 . Only N67 was close to the point of maximum recessiveness ($q \approx 100\%$). With the usual sowing density, according to results for F_1 and F_2 (see Figure 3, c and d), only W12 expressed recessiveness ($q \approx 75\%$), while the other cultivars, which did express dominance ($p \approx 50-75\%$), did not differ appreciably from one another, particularly according to the results for F_2 .

Table 4 lists data from correlation and regression analysis. A negative correlation was demonstrated between the means for the trait in the parents (\bar{x}) and level of dominance ($W_R + V_R$) in the case of low-density sowing in 1972, and a positive one with low-density sowing in 1973. Although the coefficients of correlation (r) were unreliable in most cases due to the small size of the sample ($n = 7$), they were high enough to give an idea about the phenotypic action of dominant and recessive genes.

Table 4. Results of correlation and regression analysis

Coefficient	1972			1973			
	exp-1		exp-2	exp-1		exp-2	
	\bar{x}	F_1	F_2	\bar{x}	F_1	\bar{x}	F_2
r between \bar{x} & $W_R + V_R$	-0.694	-0.775 *	-0.888 **	0.661	0.773 *	-0.683	-0.489
r between \bar{x} & W_R	0.482	0.600	0.753	0.437	0.598	0.466	0.239
r between \bar{x} & V_R	0.993 ***	0.994 ***	0.974 ***	0.995 ***	0.996 ***	0.997 ***	0.997 ***
b_{W_R/V_R}	0.916	1.003	1.121	0.820	0.906	1.001	0.988

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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The negative correlation between \bar{x} and $W_r + V_r$ indicates that, with low-density sowing in 1972 and usual density in 1972 and 1973, the positive effects on expression of the character (elongation of stem) in F_1 and F_2 hybrids are related to the action of dominant genes and negative ones (shortening of stem) to recessive genes. The positive correlation observed between these parameters in 1973 with low-density sowing indicates that positive effects on expression of the trait are related to recessive genes and negative ones, to dominant genes.

In view of the fact that the values of coefficients of determination (r^2) were significant <1 in all cases, it is not deemed purposeful to predict the limit of breeding on the basis of stem length to the maximum dominance or recessiveness of material studied. The coefficients of correlation (r') between W_r and V_r were highly reliable in all cases ($P < 0.001$). The high coefficients of regression (b) of W_r as a function of V_r indicate that the lines of regression did not deviate appreciable from the line of a single slope. This serves as additional proof of the fact that, with regard to stem length, all requirements were met in the experiment for base material, according to the hypothesis of Hayman [30].

Discussion

Our analysis shows that the genetic parameters reflecting the additive and nonadditive action of gene are characterized by considerable variability, depending on vegetation conditions (year), area of plant feeding (experiment) and generation studied (F_1 and F_2). Of particular interest is the variability of genetic parameters induced by the first two factors.

First of all, it should be noted that stem length is controlled mainly by genes with additive action, which present relative stability of phenotypic expression. Although genes with nonadditive action make a substantial contribution to the genetic system of control of the trait, they are characterized by high lability of phenotypic expression. However, the obtained data indicate that it is quite arbitrary to refer to relative stability of genetic component \hat{D} . In the case of low-density sowing (exp-1) in 1973, the value of \hat{D} was almost double the level in 1972, and in the case of usual density it was 1.5 times higher than in 1972. This occurred when no major differences were observed on the whole in stem length of cultivars and hybrids in different years and experiments. It is remarkable that there was fuller expression of genotypic differences between parents in 1973 than 1972, and it was fuller with a larger feeding area than limited one. There was even greater modification by environmental conditions of the action of genes with dominant effects. Not only did the degree of dominance fluctuate over a rather wide range, depending on meteorological conditions and plant density, these factors could also induce a change in direction of dominance. While the direction of dominance did not change in the 2 years with usual sowing density, in the case of low-density sowing component \hat{F} was characterized by a positive sign in 1972 and negative in 1973. Thus, a change in direction of dominance occurred only with the larger feeding

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area and with a shortage of water (1973). Typically enough, with the larger feeding area in 1972, positive effects (longer stem) in hybrids were related to dominant expression of gene action and in 1973, with recessive expression; therefore, the group means for F_1 hybrids were higher than for parents, in both the former and latter cases.

This study also revealed that the values of genetic components vary, depending on the generation studied. Components $\hat{\sigma}^2$, $\hat{\sigma}_1^2$, $\hat{\sigma}_2^2$ and $\hat{\sigma}^2$, which characterize allelic interaction of genes, were significantly lower according to results of evaluation of F_2 hybrids than F_1 . Moreover, in the case of usual sowing density in 1973, the values of $\hat{\sigma}_1^2$ and $\hat{\sigma}_2^2$ were unreliable according to results obtained for F_2 . Such differences, which were found in evaluating nonsegregating (F_1) and segregating (F_2) generations, are attributable to the fact that two short-stemmed cultivars, W12 and W77, were included in the experiment, and they are characterized by a specific system of genetic control of stem length. In hybrid combinations involving short-stemmed cultivars, on the one hand, and medium and long-stemmed ones, on the other, significant intrapopulation diversity occurred in F_2 with respect to phenotypic expression of the character as a result of recombination of genes controlling stem length. If we consider that there is a correlation between stem length and expression of other quantitative characters, in particular, development of the root system, we shall realize how complex the conditions, under which F_2 plants differing in stem length underwent individual development. Starting with the early stages of ontogenesis, competitiveness induced by distinctions of stem morphogenesis in different F_2 genotypes influences expression of genetic information that determines development of all traits that are directly or indirectly related to plant height. Hence, in those cases where the cultivars used in diallele crosses differ in system of genetic control of stem length, segregation automatically leads to appearance of recombinants varying in capacity for competition; therefore, it is undesirable to use F_2 hybrids in diallele analysis.

We were impressed by the fact that, in the material studied, there was a disproportion between genes with dominant and recessive action, as well as genes with positive and negative effects. Such asymmetry of distribution of genes with different types of action is apparently related to the distinctions of the system of genetic control of the trait in short-stemmed W12 and W77. It is assumed that, in hybrids obtained from crossing short-stemmed cultivars with medium and long-stemmed ones, the strong individual effects of a small number of genes controlling the short stem trait are obscured by a large number of genes with mild effects that control dominance; therefore, on the lines of regression of W_r as a function of V_r , significant intervals are not demonstrable between the short- and long-stemmed cultivars. Consequently, diallele analysis does not demonstrate the contrast in the system of genetic control of the character that is manifested by the relative expression of the trait in the cultivars.

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As we know, the objective of diallele analysis is to determine the nature of action and interaction of genes that control a certain character and, on this basis, to predict the possibilities of improving the trait through breeding within the range of the base material used in the analysis. As shown by correlation analysis of the results of evaluation of F_1 hybrids, the link between mean values of the character in the parents and level of dominance was reliable in only one case (exp-2, F_1 , 1972). But even in this case, the coefficient of determination was significantly <1 , which did not make it possible to reliably forecast the range of breeding for this character. From the standpoint of practical breeding tasks referable to a strongly continental climate, there is no need to define this range, since excessive shortness or tallness does not meet the requirements made of cultivars raised under such conditions, where years with adequate precipitation alternate with years of drought. In the presence of drought, the short-stemmed cultivars form such short plants that it is extremely difficult to use mechanized harvesting. In addition, the stubble left after harvesting plays an important erosion-control and snow-retaining role in modern agriculture in the steppe regions of Siberia. Of course, it is difficult to solve this problem using short-stemmed cultivars. However, long-stemmed ones also fail to meet the requirements of modern agriculture. In years with good precipitation, when a large harvest is expected, tall cultivars are usually subject to severe lodging under the influence of torrential rains associated with winds at the flowering and plumping stages, which leads to significant loss of harvest and also makes harvesting more difficult. Thus, the climate and intensive modern agriculture pose some very difficult problems to breeding practice. In the first place, the cultivars must have a high genetic potential for productivity, and this would be impossible without adequate resistance to lodging. In the second place, the cultivars must be drought-resistant, and they should not react by drastic reduction of stem length. Of the material studied, cultivars N67 and G114 best meet the former requirement, but they are not resistant enough to severe drought.

The high variability we demonstrated for genetic parameters must be taken into consideration in developing breeding programs for the purpose of creating cultivars with a specific plant height. Most nonlocal short-stemmed cultivars are included in breeding programs, not only as carriers of genes controlling shortness and resistance to lodging, but as sources of genes of resistance to brown and stem rust. Our study revealed that, when crossing short-stemmed cultivars with long-stemmed ones, it is desirable to grow the segregating generation of hybrids with provisions for a large plant feeding area, which enhances the effectiveness of selection for the trait in question, for the purpose of fuller expression of genetic information. However, it must be borne in mind that, in the case of low-density sowing, when there is attenuation of intergenotypic competition, there may be stronger expression of dominant effects that are not expressed when there is a limited feeding area, which intensifies such competition. It should also be borne in mind that different degrees of

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competitiveness of plants differing in height, which are genotypically determined, may lead to significant interplot interaction when evaluating genotypes at the early stages of breeding. For this reason, breeding nurseries should be made up of blocks with consideration of the expected phenotypic expression of the character, for the purpose of ruling out, if possible, or attenuating negative interaction between genotypes raised on adjacent plots. This will permit objective evaluation of breeding material, not only with respect to plant height, but other traits related to plant productivity.

If we were to consider the results obtained from the standpoint of effectiveness of selection in segregating generations, it is important to bear in mind the distinctions of the system of genetic control in different cultivars. Since the results of F_2 analysis are not reliable enough to assess the cultivars for this character, let us refer to the results obtained for F_1 . In hybrids involving medium and long-stemmed cultivars G114, N67, P28 and M553 with the usual density of plant stands, there was expression only of dominance to varying extents in the direction of the parent with the longer stem, whereas in the case of low-density stands we observed a change in direction of dominance induced by vegetation conditions (year). Consequently, in hybrids involving these cultivars, there was more stable expression of dominance of direction of action when they were raised with a limited feeding area. On this basis, it may be assumed that, in hybrids involving G113, N67, M553 and P28, in the early segregating generations the dominant alleles inducing elongation of the stem overlap recessive alleles that shorten the stem. However, in view of the fact that genes with additive action make the main contribution to development of the stem, selection for plant height can be started in early segregating generations (F_2 , F_3). But it must be borne in mind that genotypes selected in early generations may segregate in later generations when these cultivars are crosses with short-stemmed ones, such as W12 and W77. It is also important to take into consideration the fact that there is stronger manifestation of effects, both with regard to expression and direction of action, when segregating generations are raised under conditions of larger feeding areas.

To conclude our discussion of the experimental data we obtained, we must call attention to one substantial distinction of the system of genetic control of stem formation, which is the variability of relative contribution of dominant and recessive alleles to phenotypic expression of the trait in hybrids. The following question remains open: Does the nature of allele action change, expressing dominance under some conditions or recessiveness under others, or are different genes in the system of control of stem morphogenesis included or excluded during ontogenesis, depending on ambient conditions? We can only assume that both phenomena occur in the system of genetic control of this quantitative character. The difficulty lies in the fact that variability of genetic parameters as a function of environmental conditions does not allow us to obtain an

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unequivocal answer concerning the nature of inheritance of the character, and this makes it difficult or impossible to predict the effectiveness of selection in segregating generations.

BIBLIOGRAPHY

1. Tsil'ke, R. A. "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 1: Stem Length," GENETIKA [Genetics], Vol 11, No 2, 1975, 14.
2. Borojevic, S. "Type of Inheritance and Heritability of Quantitative Traits in Hybrids of Different Wheat Cultivars," SAVREMENA POLJOPR. Modern Agriculture (Croatian)], Vol 13, No 7-8, 1965, 587.
3. Idem, "Characteristics of Some New Dwarf and Semidwarf Wheat Lines," EUPHYTICA, Vol 17, Suppl No 1, 1968, 143.
4. Karamyshev, R. M. "Some Distinctions of Inheritance of Plant Height in Soft Wheat (*T. aestivum* L.)," "Collection of Works of Graduate Students and Young Scientists," Leningrad, All-Union Scientific Research Institute of Plant Growing imeni N. I. Vavilov, Vol 7(11), 1966, 37.
5. Powell, J. B., and Schlehuber, A. M. "Components of Height Inheritance of the Semidwarf Straw Character in Wheat *Triticum aestivum* L.," CROP SCI., Vol 7, No 5, 1967, 511.
6. Piech, J., and Evans, L. E. "Inheritance of Dwarfing in Crosses of Spring Wheat Varieties," GENETICA POLON., Vol 8, No 1-2, 1967, 1.
7. Rehman, A. A., and Rehman, C. A. "Heritability and Inheritance of Plant Height, Heading Date and Grain Yield in Four Spring Wheat Crosses," CROP SCI., Vol 9, No 6, 1969, 760.
8. Allan, R. E.; Vogel, O. A.; and Peterson, C. J. "Inheritance and Differentiation of Semidwarf Culm Length of Wheat," Ibid, Vol 8, No 6, 1968, 701.
9. Briggles, L. W., and Vogel, O. A. "Breeding Short-Stature Disease-Resistant Wheats in the United States," EUPHYTICA, Vol 17, Suppl No 1, 1968, 107.
10. Reddy, M. V.; Heyne, E. G.; and Liang, G. H. L. "Heritabilities and Interrelationships of Shortness and Other Agronomic Characters in F₃ and F₄ Generations of Two Wheat Crosses (*Triticum aestivum* L. em. Thell), " CROP SCI., Vol 9, No 2, 1969, 222.

FOR OFFICIAL USE ONLY

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11. Walton, O. D. "Inheritance of Morphological Characters Associated With Yield in Spring Wheat," CANAD. J. PLANT SCI., Vol 49, No 5, 1969, 587.
12. Reddy, M. V., and Heyne, E. G. "Inheritance of Plant Height and Kernel Weight in Two Wheat Crosses," INDIAN J. GENET. AND PLANT BREED., Vol 30, No 1, 1970, 109.
13. Anand, S. C., and Aulakh, H. S. "Inheritance of Dwarfness in Olesen's Dwarf (T. aestivum L.)," WHEAT INFORM. SERV., Vol 32, 1971, 14.
14. Nalepa, S. "Inheritance of Dwarf Character in Wheat," POSTEPY NAUKI ROLN. [Advances in Agricultural Science (Polish)], No 4, 1971, 15.
15. Rachinski, T. "Inheritance of Culm Height and Spike Productivity in Intervarietal Soft Wheat Hybrids," GENETIKA I SELEKTSIYA (NRB) [Genetics and Plant Breeding (Bulgarian)], Vol 4, No 6, 1971, 369.
16. Khadr, F. H. "Variability and Covariability for Plant Height, Heading Date and Seed Weight in Wheat Crosses," THEOR. AND APPL. GENET., Vol 41, No 3, 1971, 100.
17. Khadr, F. H.; Ismail, A. M.; and Morsy, M. S. "Heritabilities of Quantitative Traits Estimated by Different Methods in Generations of Wheat Crosses," EGYPT. J. GENET. AND CTYOL., Vol 1, No 2, 1972, 263.
18. Zhumazhanov, Zh. "Heritability of Stem Height in Crosses of Spring Wheat," in "Biologiya i geografiya" [Biology and Geography], Alma-Ata, Kaynar, Vyp 7, 1972, p 31.
19. Amaya, A. A.; Busch, R. H.; and Lebsock, K. L. "Estimates of Genetic Effects of Heading Date, Plant Height and Grain Yield in Durum Wheat," CROP SCI., Vol 12, No 4, 1972, 478.
20. Rajinder, K.; Anand, S. C.; and Virk, D. S. "Heritability and Genetic Advance of Some Quantitative Characters in Crosses of Wheat (Triticum aestivum L.)," J. RES., Vol 9, No 4, 1972, 515.
21. Villanueva, N. R. "Inheritance of Height and Other Characters Under Conditions of the Coast of Peru," "Proc. 4th Int. Wheat Genet. Sympos.," Columbia, Mo., 1973, p 611.
22. Gulyan, A. A. "Inheritance of Some Quantitative Characters in Winter Wheat," "Tekhekagir gyukhatntesakan gitutyunner" [News in Agricultural Sciences], No 4-5, 1974, 43.
23. Tsil'ke, R. A. "Variability of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1974, 31.

FOR OFFICIAL USE ONLY

24. Ingold, M. "Culm Length in F₁ Wheat Hybrids (*Triticum aestivum* L.)," SCHWEIZ. LANDWIRT. FORSCH., Vol 13, No 1-2, 1973, 235.
25. Halloran, G. M. "Genetic Analysis of Plant Height in Wheat," THEOR. AND APPL. GENET., Vol 45, No 8, 1975, 368.
26. Fedin, M. A.; Lyameborshay, L. M.; and Silis, D. Ya. "Use of Diallele Crosses in Genetic Analysis of Plant Height Trait," DOKL. VASKhNIL [Reports of the All-Union Academy of Agriculture imeni Lenin], No 5, 1972, 3.
27. Siraj-Ud-Din, S., and Muhammad, S. "Inheritance of Response of Six Wheat Varieties to Two Density Conditions Under Three Sowing Dates," PAKISTAN J. SCI., Vol 24, No 1-2, 1972, 9.
28. Khadr, F. H.; Kassem, A. A.; and Elkhishen, A. A. "Hill Versus Row Plot for Testing Wheat Lines," CROP SCI., Vol 10, No 4, 1970, 449.
29. Tsil'ke, R. A.; Kachur, O. T.; and Sadykova, S. A. "Variability of Genetic Parameters in Diallele Analysis of Quantitative Characters of Soft Spring Wheat. Report 1: Number of Spikelets per Spike," GENETIKA, Vol 14, No 8, 1978, 1409.
30. Hayman, B. I. "The Theory and Analysis of Diallele Crosses," GENETICS, Vol 39, 1954, 789.
[485-10,657]

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CSO: 8144/0485

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VARIABILITY OF GENETIC PARAMETERS IN DIALLELE ANALYSIS OF QUANTITATIVE
CHARACTERS OF SOFT SPRING WHEAT. REPORT 3: SPIKE LENGTH

Moscow GENETIKA in Russian Vol 15, No 2, 1979 pp 286-297

[Article by R. A. Tsil'ke, O. T. Kachur and S. A. Sadykova, Siberian
Scientific Research Institute of Agriculture, Omsk, submitted 13 Oct 77]

[Text] A diallele analysis was made of seven soft spring cultivars for spike length. It was shown that the parameters that characterize the system of genetic control of this trait vary significantly, depending on vegetation conditions (years), density of plant stands and generation of hybrids studied. This character is controlled by an additive-dominant genetic system. The variability of genetic parameters makes it difficult to predict improvement of this character by means of breeding.

The worldwide pool of soft wheat genes is characterized by considerable diversity of spike length. The degree of expression of this trait fluctuates over a wide range, depending on geographic and climatic conditions, and direction of breeding. Much attention is given to spike length in modern breeding programs, since it is correlated with other structural elements that determine spike productivity. Genetic studies pursued in different climates and on different base material revealed that spike length is controlled by a large number of genes with different types of action and interaction. A recent survey of works published on the nature of inheritance of this character [1] relieves us of the task of repeating an analysis of the studies that have been conducted. Let us merely note that spike length is controlled chiefly by genes with additive action. At the same time, it was also demonstrated that genes with dominant and recessive effects have a significant influence on development of this character in hybrids.

Under the conditions of Siberia, several experiments were conducted [1, 2] and showed that the nature of expression and inheritance of this trait varies, depending on vegetation conditions (years). This, of course, makes it difficult to predict the effectiveness of selection in segregating

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generations. Since importance is attributed to spike length, which is modified to some extent by environmental factors, when selecting plants for spike productivity under field conditions, our objective was to study variability of the parameters characterizing the system of genetic control of this trait, as related to area of plant feeding, meteorological conditions and hybrid generation studied. In this article, we submit the results of diallele analysis of spike length, which were obtained under different vegetation conditions (years) and different plant feeding areas (experiments).

Material and Methods

The following cultivars were used in diallele analysis: Saratovskaya 29 (S29), Mil'turum 553 (M553), Novosibirskaya 67 (N67), Grecum 114 (G114), Pirotriaks 28 (P28), World Seeds 1877 (W77) and World Seeds 1812 (W12). These cultivars differ substantially, not only in spike length but some other economically valuable characters. S29 is characterized by high drought resistance and grain quality; M553 is adapted to the dry steppe conditions of Siberia; P28 has a high genetic potential for general productivity; N67 and G114 are resistant to lodging and highly productive; the American short-stemmed varieties, W12 and W77, are resistant to lodging and rust fungi.

The cultivars, F_1 and F_2 hybrids were raised under field conditions in two experiments in 1972 and 1973, which differed in plant feeding area: experiment 1 (exp-1), with low-density sowing and 10×40 cm (400 cm^2) feeding area and experiment 2 (exp-2), with usual sowing density and feeding area of 2×20 cm ($\approx 40 \text{ cm}^2$). When scaled to 1 m^2 , the number of germinative seeds constituted 25 in exp-1 and 250 in exp-2. We excluded from structural analysis plants that were raised with a regional [marginal] effect. Tests for homogeneity of $W_r - V_r$ revealed that the base material conformed with the requirements stipulated according to the hypothesis of Hayman [3], with respect to spike length. The details on the experimental methods, characteristics of base material and data about meteorological factors were given in our previous report [4].

Experimental Section

Table 1 lists the mean values for the trait in parents and hybrid groups derived from each parent. The varieties used in the experiment differed appreciably in spike length. Vegetation conditions and plant feeding area had a significant influence on degree of expression of this trait. In 1972, spike length ranged from 84.8 (W77) to 112.0 (G114) in the cultivars, and in 1973 from 70.8 (W12) to 112.5 mm (G114) in exp-1; in the case of the usual sowing spacing (exp-2), the figures were 73.5 to 105.7 and 61.5 to 81.0 mm, respectively.

As we see, with the larger area of plant nutrition, the cultivars and hybrids formed a longer spike than with a limited area, and they formed a

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longer stem in 1972 than 1973. The differences in spike length between short-stemmed early-ripening W12 and W77, as well as between long-stemmed late-ripening M553 and P28, were less marked than between average ripening and average height cultivars S29, N67 and G114, which occupy an intermediate position in relation to the short- and long-stemmed varieties. While G114 formed the shortest stem in the group of cultivars of medium height [5], it was considerably superior to all other varieties tested in this experiment with respect to spike length. The group means (\bar{X}) for F_1 hybrids were higher in all cases than the group means for parents, which is indicative of expression of dominant effects. In the case of low-density sowing (exp-1), the differences were more marked between group means for hybrids and parents than in the case of usual sowing density (exp-2). Negligible differences were observed between the group means for F_1 and F_2 hybrids.

Table 1. Spike length in parents (\bar{x}) and hybrids (x_0), mm

Variety	1972						1973					
	exp-1			exp-2			exp-1			exp-2		
	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2	P	F_1	F_2
W 12	85.4	100.2	100.4	74.5	84.8	70.8	83.6	81.2	61.5	68.6	69.3	
W 77	84.8	100.4	99.9	73.5	82.9	71.9	83.4	80.7	63.8	69.5	67.0	
S 29	98.0	105.3	103.9	82.8	87.7	85.0	89.3	87.9	63.2	69.1	68.0	
N 67	104.7	109.1	107.3	92.2	90.9	93.0	93.8	90.4	66.2	70.5	69.6	
G 114	122.0	116.8	114.7	105.7	97.5	112.5	101.1	98.4	81.0	75.9	74.8	
M 553	118.6	112.0	112.3	94.4	93.3	97.4	94.6	94.5	68.8	69.7	68.9	
P 28	118.8	114.6	114.3	101.1	95.9	105.1	98.5	98.3	74.0	73.1	73.0	
(\bar{x})	104.8	108.3	107.6	89.2	90.4	90.8	92.0	90.2	69.4	70.9	69.9	
HCP with $P < 0.05$		4.71		1.90			4.28		2.28			

Table 2. Results of variance and covariance analysis

Parameters	1972			1973			
	exp-1		exp-2	exp-1		exp-2	
	F_1	F_2	F_3	F_1	F_2	F_1	F_2
\hat{D}	240.12 ***	238.34 ***	158.44 ***	244.34 ***	243.95 ***	45.21 ***	45.67 ***
\hat{P}	-6.73 *	-1.50	-14.27 ***	-27.32 ***	-48.81 ***	3.36 *	0.17
\hat{H}_1	18.70 ***	-0.21	5.78 **	7.06 *	0.93	3.82 *	2.02
\hat{H}_2	18.04 **	3.42	6.41 **	12.10 **	1.81	4.87 *	1.42
\hat{H}_3	34.97 ***	23.77 **	3.25 **	0.47	3.22	17.06 ***	5.84 ***
$(\hat{H}_1/\hat{D})^2$	0.28	...	0.19	0.17	...	0.29	...
H_2/H_1	0.24	...	0.28	0.43	...	0.32	...
$(4\hat{D}\hat{H}_1)^2 + \hat{P}$	0.90	...	0.82	0.50	...	1.29	...
$(4\hat{D}\hat{H}_1)^2 - \hat{P}$							
\hat{E}	4.06 *	5.84 *	2.70 **	8.28 ***	8.87 **	3.56 *	3.10 **

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ... - indices were not calculated due to unreliability of one of base parameters.

Table 2 lists the results of variance and covariance analysis. Component \hat{D} , which reflects the contribution of genes with additive action to the system of genetic control of the trait has a significantly higher value

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than components indicative of dominant gene action. With low-density sowing (exp-1), the values of \hat{D} did not differ in different years, whereas with usual sowing density (exp-2) they were 3.5 times higher in 1972 than 1973. The values of component \hat{F} , which reflects the direction of dominance as a whole for all hybrids, were reliable in all cases according to results of estimates of F_1 hybrids, and this index was characterized by a negative sign in both experiments in 1972, whereas in 1973 it was negative in the case of low-density sowing and positive, with usual sowing density. In the case of positive values for \hat{F} , the dominant effects induce elongation of the spike and with negative values, shortening. According to results of estimates of F_2 hybrids, the values of genetic parameters \hat{F} , \hat{H}_1 and \hat{H}_2 were unreliable in most cases; for this reason we did not calculate such indices as mean degree of dominance, proportion of genes with positive and negative effects, as well as proportion of dominant and recessive alleles. These indices were calculated for all experiments from the results of evaluation of F_1 hybrids. The index of mean degree of dominance constituted 0.28 in 1972 and 0.17 in 1973 for exp-1, 9.19 and 0.29, respectively for exp-2, which is indicative of partial dominance manifested to different degrees in F hybrids. Parameter $\hat{H}_2/4\hat{H}_1$, which reflects the proportion of genes with positive and negative effects, was close to the 0.25 level (0.24) only in the case of low-density sowing in 1972, whereas with usual sowing density that year it constituted 0.28, the figures being 0.43 with low-density sowing and 0.32 with usual sowing in 1973. This index, as we see, deviated significantly from the above level, which was indicative of a dissimilar number of genes among parents manifesting positive and negative effects. Index $(4\hat{D}\hat{H}_1)^{1/2} + \hat{F} / (4\hat{D}\hat{H}_1)^{1/2} - \hat{F}$, which reflects the proportion of total number of dominant alleles to total number of recessives in all parents, constituted 0.90 in 1972 and 0.50 in 1973 with low-density sowing, 0.50 and 1.29, respectively, with usual sowing density. As we see, in the case of a limited feeding area (exp-2) in 1972 and enlarged one in 1973, there was an excess of recessive alleles, and with the limited feeding area in 1973 there was an excess of dominant ones. This disproportion was also confirmed by the values of index \hat{F} .

As shown by the data in Table 3, parameter \hat{F}_R was reliable in most cases, according to estimates of both F_1 and F_2 hybrids. This parameter reflects the relative contribution of dominant and additive genes to development of the trait in the group of hybrids derived from each parent. The obtained data indicate that the value of \hat{F}_R fluctuates markedly, depending on vegetation conditions, plant feeding area and generation studied.

The genetic system of control of the trait in each cultivar, in particular, the relative contribution of dominant and recessive alleles, are graphically illustrated by the curves of regression of W_R as a function of V_R (Figures 1 and 2). Let us mention that the line of regression is significantly higher than the start of the coordinates on all of the graphs. This confirms the conclusion that there is expression of partial dominance for spike length in the hybrids as a whole. In 1972, according to the results

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of evaluation of F_1 (see Figure 1a), cultivars G114, S29 and M553 expressed recessiveness ($q \approx 50-75\%$). W77 and P28 expressed negligible dominance, W12 and N67 expressed neither dominance nor recessiveness. According to the estimates for F_2 , in this experiment N67 and G113 did not manifest dominant effects (see Figure 1b); P28 and M553 expressed dominance ($p \approx 75\%$), while W12 and W77 expressed recessiveness ($q \approx 75-100\%$). With the usual density of plant stands (exp-2), in 1972 G114, N67 and S29 manifested recessiveness ($q \approx 50-75\%$), W77 and P28 presented dominance ($p \approx 50-75\%$), while W12 and M553 did not express these effects according to results for F_1 (see Figure 1c). In 1973, with the larger plant feeding area (exp-1), M553, S29 and P29 expressed significant recessiveness ($q \approx 75\%$), G114 expressed almost complete recessiveness ($q \approx 100\%$), while there was considerable dominance ($p \approx 50-75\%$) for W12, W77 and N67 according to F_1 estimates (see Figure 2a). According to results for F_2 (see Figure 2b) in this experiment, there was negligible dominance expressed in W77 and N67 and recessiveness in P28, M553 and S29 ($q \approx 50-75\%$); G114 presented complete recessiveness. With the usual feeding area (exp-2) in 1973, according to results for F_1 (see Figure 2c), W77 and S29 did not express either dominance or recessiveness; G114, P28 and M553 expressed dominance ($p \approx 50-75\%$), W12 and N67 expressed recessiveness ($q \approx 50-75\%$). According to the results for F_2 in this experiment (see Figure 2d), there was expression of dominance ($p \approx 50-75\%$) in W77, S29 and N67, and negligible recessiveness in W12, G114 and P28. The regression curves are specially rendered on the same scale, in order to emphasize the variability of variances and covariances as a function of density of plant stands.

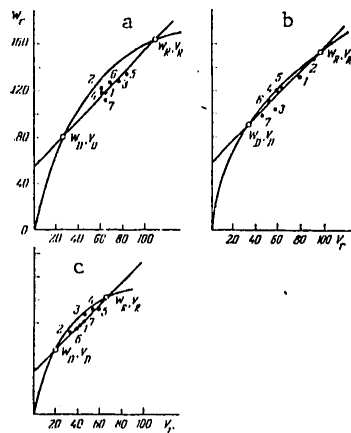


Figure 1.
Regression curves for W_r as a function of V_r in 1972

- | | |
|------------------|------------------|
| a) F_1 , exp-1 | c) F_1 , exp-2 |
| b) F_2 , exp-1 | |
| 1) W12 | 5) G114 |
| 2) W77 | 6) M553 |
| 3) S29 | 7) P28 |
| 4) N67 | |

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Table 3. Results of estimates of \hat{F}_r

Parent	1972			1973 r.			
	exp-1		exp-2	exp-1		exp-2	
	F_1	F_2	F_3	F_1	F_2	F_1	F_2
W 12	9.82	-52.67 *	4.99	85.10 ***	9.39	-17.60 *	-5.83 *
W 77	13.36 *	-105.84 *	33.38 *	47.71 **	43.49 **	-0.03	15.50 *
S 29	-30.84 *	24.65	-23.78 *	-87.85 ***	-55.69 **	-2.72	7.94 *
N 87	12.43	5.57	-48.42 *	28.97 *	23.59 *	-11.82 *	8.29 *
GI 14	-59.23 *	-0.22	-50.50 *	-158.13 ***	-223.89 ***	22.91 *	-12.22 *
M 553	-14.16 *	43.01 *	8.91	-42.94 *	-103.58 ***	6.81 *	-1.05
P 28	21.50 *	74.96 **	-14.39 *	-84.18 ***	-34.98 *	20.13 *	-11.51 *

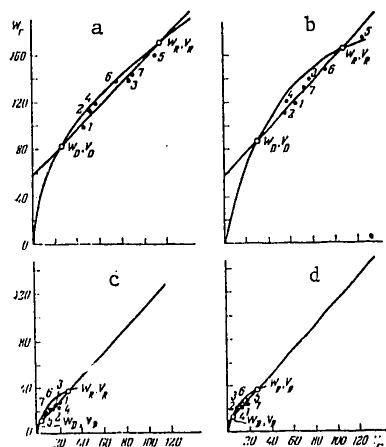
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 2.

Regression curves for W_r as a function of V_r in 1973. Designations are the same as in Figure 1.

- a) F_1 , exp-1 c) F_1 , exp-2
b) F_2 , exp-1 d) F_2 , exp-2

The data listed in Table 4 indicate that, according to F_1 estimates, the link between mean values for the character in parents (\bar{x}) and level of dominance ($W_r + V_r$) was reliable only in 1973, the coefficient being positive ($r = 0.869$) with the larger feeding area and negative ($r = -0.871$) with the limited one (exp-2). According to the F_2 estimates, the link between these two indices was reliable in exp-1 1972 ($r = -0.800$) and exp-1 1973 ($r = 0.759$). In all cases, the coefficient of determination (r^2) was significantly < 1 . The coefficients of correlation (r') between W_r and V_r were highly reliable in all cases ($P < 0.001$), while the lines of regression of W_r as a function of V_r did not deviate appreciably from the line of a single slope.

Discussion

Our diallele analysis revealed that spike length in the cultivars studied is controlled by an additive-dominant genetic system, the genes with additive action making the larger contribution to this system. It was established that the values of the genetic parameters fluctuate over a rather wide range, depending on vegetation conditions (year), density of plant stands (experiment) and hybrid generation (F_1 and F_2) studied. The variability of these parameters is related primarily to lability of expression of the character and genotype \times environment interaction. Along with similarity of quantitative traits, according to nature of expression

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and inheritance, we also demonstrated certain differences between them, and this could not fail to affect the results of diallele analysis. While the cultivars and their hybrids formed a shorter stem in 1972 than 1973, and a shorter one with low-density sowing than ordinary density [5], the reverse was observed with respect to number of spikelets [4], and this was typical for the trait in question also. In 1972, the cultivars and hybrids formed a longer head than in 1973, and a longer one with the larger feeding area than the usual area.

Table 4. Results of correlation and regression analysis

Coefficients	1972			1973			
	exp-1		exp-2	exp-1		exp-2	
	F_1	F_2	F_3	F_1	F_2	F_3	F_4
r between \bar{x}	0,418	-0,800 *	0,682	0,869 **	0,759 *	-0,871 **	0,681
r between \bar{x} and W, V, V_2	0,173	0,010	0,405	0,755	0,578	0,759	0,477
r between V, V_2 and W, V_2	0,867 ***	0,993 ***	0,888 ***	0,887 ***	0,902 ***	0,960 ***	0,918 ***
b_{W, V, V_2}	0,952	0,098	1,046	1,009	1,114	1,106	1,104

* $P < 0,05$; ** $P < 0,01$; *** $P < 0,001$.

It is remarkable that genetic component \hat{D} for stem length and number of spikelets per spike fluctuated in different years and experiments [4, 5], whereas for spike length its value was the same in different years in the case of larger plant feeding area (exp-1), but different with the usual feeding area (exp-2). Thus, with the usual area, the value of component \hat{D} was 3.5 times higher in 1972 than 1973. The obtained results clearly show that parameter \hat{D} , which reflects the contribution of genes with additive action to development of the trait, is more stable in different years with the enlarged feeding area, when there was more complete expression of genetic potential for phenotypic manifestation of the character. The significant fluctuation of \hat{D} in different years in the case of limited plant feeding area is, apparently, related to the fact that with such sowing genotypic differences are not fully manifested. Here, the reaction of the genotype to environmental conditions played a very important role. Parameter \hat{F} , which reflects the direction of dominance as a whole for all hybrids, varied considerably more than \hat{D} in different years and experiments. While \hat{F} was characterized by a negative value according to stem length only with low-density sowing in 1973 and according to number of spikelets in all experiments [4], according to spike length it had such a value in both experiments in 1972 and exp-1 in 1973. Consequently, it was only with a limited feeding area (exp-2) under the conditions of 1973 that \hat{F} was characterized by a positive value, its value in exp-2 according to F_1 estimates being 8 times lower than in exp 1, and in 1972 twice as high in exp-2 than exp-1. Such variability of parameter \hat{F} is indicative of sensitivity of the system of genetic control of the trait, particularly the genes that express allele interaction. Parameters \hat{H}_1 and \hat{H}_2 , which reflect

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interaction of genes that have positive and negative effects, also fluctuated over a wide range, depending on the year, experiment and generation. According to evaluation of F_1 , the values of \hat{H}_1 and \hat{H}_2 differed reliably in the 1973 experiments. This shows that there was expression of inequality of alleles with positive and negative effects in the material tested, and this is confirmed by parameter $\hat{H}_2/4\hat{H}_1$, which deviated significantly in these experiments from the 0.25 level. This disproportion was particularly evident in the F_1 estimates in the case of low-density sowing in 1973. We were impressed by the fact that, according to F_2 evaluations, parameters \hat{H}_1 and \hat{H}_2 were unreliable in all cases for this trait, whereas they were reliable in all experiments for number of spikelets [4].

The proportion of total dominant alleles to total recessives as a whole for all parents shows that there was an excess of recessive alleles in 1972 with the usual feeding area and 1973 with the enlarged area, and an excess of dominant ones in 1973 with the usual plant feeding area. Thus, vegetation conditions and density of plant stands had a substantial influence on expression of genetic information, as manifested by variability of proportion of alleles with different types of action. The fact that the parameters reflecting allelic gene interaction (\hat{H}_1 and \hat{H}_2) were unreliable according to F_2 findings indicates that recombination of genes leading to redistribution of genetic effects in the segregating generation influenced the mean value of the trait in F_2 , on the basis of which variance and covariance analysis was made. The appreciable deviations of F_2 means from F_1 means for spike length, which were observed in some hybrids, caused a significant change in the results of analysis of F_2 . These deviations were related primarily to the fact that competition developed in segregating F_2 populations, among hybrids involving short- and long-stemmed cultivars, as a result of recombination of genes controlling stem length, between plants characterized by different heights; this, in turn, affected expression of genetic information determining development of quantitative traits functionally related to stem length. The consequences resulting from crossing short-stemmed cultivars with long-stemmed ones were discussed in detail in a previous report [5]. They amount to the fact that the results of evaluation of F_2 do not differ appreciably from those of F_1 , and therefore use thereof in diallele analysis is not recommended.

Parameters \hat{D} , \hat{F} , \hat{H}_1 , \hat{H}_2 and the indices calculated on their basis yield only a general idea about the system of genetic control of the character in the assortment of cultivars studied. In order to solve practical breeding problems, it is very important to have information about the genetic system of each cultivar included in the analysis. Such information can be obtained from the results of estimating parameter \hat{F}_r , which is graphically illustrated by the lines of regression of W_r as a function of V_r . The obtained values for \hat{F}_r indicate that there were considerable differences between cultivars in relative contribution of genes with additive and dominant action. Expressly this parameter reflects the most fully the distinctions of inheritance of the trait, which are due,

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on the one hand, to the nature of variability of phenotypic expression thereof and, on the other hand, interaction arising between the genotype and environment in the course of ontogenesis. According to F_1 estimates, none of the tested cultivars was characterized by high stability of parameter \hat{F}_r . Moreover, the same (negative) values of \hat{F}_r were obtained only for cultivar S29, and even there the value was unreliable in one case. In all other cultivars, we observed not only a change in direction of dominance, but significant fluctuation of value of \hat{F}_r in different years, experiments and generations. G114 was characterized by the highest value of F_r ; in this cultivar, this parameter was highest for both stem length and number of spikelets per spike [4, 5]. However, the difference consisted of the fact that parameter \hat{F}_r , for both spike length and number of spikelets per spike, was characterized by a negative value and, for stem length, by a positive one in both 1972 experiments and the one with the usual sowing density in 1973. These differences in the system of genetic control of different characters in G114 must be taken into consideration when using it in breeding programs. In the other cultivars, the genetic system of control of the trait in question was modified even more by environmental conditions. It is quite obvious that such variability of genetic parameters makes it difficult to evaluate cultivars as sources of valuable genes and cross components. However, before making such an evaluation, one must determine the link between degree of expression of the traits in cultivars and level of dominance ($W_r + V_r$), which makes it possible to obtain information about the nature of influence of genes expressing allelic interaction on development of the character. From the results obtained for F_1 , these links are reliable only in the 1973 experiments, the coefficient of correlation being positive with low-density sowing and negative with the usual density. Since a positive link indicates that the positive effects that make the spike longer are induced by recessive genes and negative ones by dominant ones, selection can be effective only in late segregating generations, when there is segregation of recombinants containing the maximum number of genes with recessive expression. However, it is also difficult to predict the effectiveness of breeding for this trait due to the fact that, in 1973, the coefficient of correlation between \bar{X} and $W_r + V_r$ was positive in the case of low-density sowing and negative with the usual density, i.e., in the latter case the positive effects were related to dominant gene action and the negative ones to recessive action.

The relevant calculations according to Hayman [3] were made to predict the range of breeding improvement of the trait on the basis of the material studied; they revealed that the expected maximum spike length is 116 mm according to the results obtained in the experiment with enlarged plant feeding area and 84 mm with the usual area; in the former case, improvement of the trait should be related to recessive genes and in the latter, to dominant ones. In actuality, the longest spike was formed under these conditions by cultivar G114: 112.5 mm long with low-density sowing and 81.0 mm with the usual density. The cultivars studied can be used to upgrade this extremely important character, which is closely related to spike productivity.

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It should be noted that the new cultivars G114 and P28, recently introduced in Siberia, are characterized by a longer and more productive spike than old cultivars, along with their other positive traits. At the same time, it is apparent that short-stemmed W12 and W77, as well as S29, which is raised extensively in Siberia, cannot serve as sources of genes to upgrade the trait in question, whereas G113, P28, N67 and M553 can be used with success for this purpose. It is, however, important to bear in mind that these cultivars differ in system of genetic control of the character; therefore it is necessary to elaborate the appropriate breeding programs. While these differences are not so substantial between P28, N67 and M553, there is particularly distinct manifestation in G114 of the specific nature of inheritance of the trait, consisting of the fact that recessive genes with positive effects have a significant influence on development of the character.

In spite of the unfavorable prognosis for improvement of the trait by breeding, due to variability of the nature of allelic interaction of genes with different sowing densities, the task of further improving this character is simplified by the fact that genes with additive action play the decisive role in the system of genetic control. Since analysis revealed that the cultivars differ appreciably in expression of the trait, due to the genetic system of control in which the additive action of genes is of prevalent significance, there are grounds to expect significant positive, transgressive segregation in hybrid populations. It is expected that selection in segregating generations of hybrids derived from G114 and P28 will be the most effective. In view of the fact that genes with recessive action make a substantial contribution to the system of genetic control of the trait in G114, one should start selection among segregating generations of hybrids involving this cultivar in F_3 or F_4 , when a sufficient number of homozygous recombinants is accumulated in the population for recessive genes controlling spike length. In hybrids involving N67, P28 and M553, one can start selection in F_2 , since allelic gene interaction plays a negligible role in the genetic system and genes with additive action are of predominant significance.

As shown by analysis, the most effective selection is expected when the plants are raised with an enlarged feeding area. And this is where we come up against one of the most complex problems, which is related to the use of results of genetic analysis in breeding practice. Our study shows that there is more distinct manifestation of the distinctions of the genetic control system when the area of plant feeding is enlarged, and there is fuller expression of the genetic potential, as compared to a limited feeding area. We also know from our experience that selection and evaluation of breeding material at the early stages are usually made with reduced sowing norms, i.e., enlarged plant feeding area, whereas testing of lines for yield is conducted with a higher norm for seed sowing. We see here an overt contradiction: the types of gene action and interaction in the case of low-density sowing and extent

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thereof cannot be manifested in stands planted at the conventional density. The rather high norms for planting seeds under industrial conditions are attributable to the existence of a number of agrotechnical requirements, which by no means take into consideration the nature of the genetic system of control of formation of elements of harvest structure. Hence, either genetic analysis and, consequently, selection of genotypes must be made for higher density of plant stands, with consideration of agrotechnical sowing norms and then a significant part of the genetic information of the genotype will not be expressed, or else one must perform analysis and selection with a lower sowing density, but then there would be the task of developing a new technology for raising the cultivars. Probably, the latter route is more promising for a number of genetic, breeding, plant-growing and economic reasons. But this has yet to be proven for specific geographic and climate zones.

BIBLIOGRAPHY

1. Tsil'ke, R. A. "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses,. Report 3: Spike Length," GENETIKA [Genetics], Vol 13, No 2, 1977, 197.
2. Idem, "Variability of Inheritance of Quantitative Characters in Soft Wheat as Related to Vegetation Conditions," SIB. VESTN. S.-KH. NAUKI [Siberian Vestnik of Agricultural Science], No 2, 1974, 31
3. Hayman, B. I. "The Theory and Analysis of Diallele Crosses," GENETICS, Vol 39, 1954, 789.
4. Tsil'ke, R. A.; Kachur, O. T.; and Sadykova, S. A. "Variability of Genetic Parameters in Diallele Analysis of Quantitative Characters of Soft Spring Wheat. Report 1: Number of Spikelets per Spike," GENETIKA, Vol 14, No 8, 1978, 1409.
5. Idem, "Variability of Genetic Parameters in Diallele Analysis of Quantitative Characters of Soft Spring Wheat. Report 2: Stem Length," Ibid, this issue, p 273.
[485-10,657]

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VARIABILITY OF GENETIC PARAMETERS IN DIALLELE ANALYSIS OF QUANTITATIVE CHARACTERS OF SOFT SPRING WHEAT. REPORT 4: NUMBER OF KERNELS PER SPIKE

Moscow GENETIKA in Russian Vol 15, No 3, 1979 pp 488-497

[Article by R. A. Tsil'ke; O. T. Kachur; and S. A. Sadykova, Siberian Scientific Research Institute of Agriculture, Omsk, submitted 29 Dec 77]

[Text] Diallele analysis revealed that there is expression of variability of genetic parameters, depending on vegetation conditions (year), plant feeding area (experiment) and generation (F_1 and F_2) studied. Along with additive action, there is also manifestation of significant dominant gene action in the system of genetic control of the character.

The values of component \hat{D} , which reflects the additive action of genes, is stable in different years in the case of an enlarged plant nutrition area, but they vary significantly with the usual feeding area. The genetic components characterizing allelic gene interaction fluctuate significantly in different years and experiments.

It was demonstrated that the order of the cultivars on lines of regression of W_r as a function of V_r is subject to less change according to number of kernels per spike than spike length and number of spikelets per spike.

Forecasting improvement of the trait by breeding revealed that the expected maximum effect does not exceed the level attained in cultivar P28, which is considerably superior to the others in number of kernels per spike and for this reason is a unique source of genes that control spike productivity.

The productivity of a spike is directly related to the number and weight of kernels formed in it. These characters are controlled by a complex genetic

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system that interacts closely with environmental conditions during ontogenesis. The worldwide pool of genes of soft spring wheat is characterized by considerable diversity of number of kernels per spike, which is attributable to the direction of selection and geographic-climate conditions under which the cultivars are developed and raised. However, it is assumed that the genetic potential of hexaploid wheat has not yet been realized in modern cultivars. The variability of nature of expression of the trait, which is related to sensitivity of morphogenesis of generative organs in the ontogenetic process, creates a number of difficulties in improving the trait through breeding and realizing its genetic potential when the cultivars are grown under industrial conditions.

A significant number of studies has been pursued in our country and abroad on the nature of inheritance of the character in question. But since a survey of these studies has been recently published [1], there is no need to repeat it here. It was shown that the character is controlled by a large number of genes, the action and interaction of which are strongly modified by environmental conditions. The conclusions of researchers concerning the system of genetic control of the character are quite contradictory, and this is attributable to variability of its expression and genotypic diversity of material used in genetic analysis.

Our objective was to study the variability of parameters characterizing the system of genetic control of the trait as related to vegetation conditions (year), plant feeding area (experiment) and hybrid generation (F_1 and F_2) analyzed. In this article we report the results of diallele analysis of number of kernels per spike.

Material and Methods

The following cultivars were included in diallele analysis: Saratovskaya 29 (S29), Mil'turum 553 (M553), Novosibirskaya 67 (N67), Grecum 114 (G114), Pirotriaks 28 (P28), World Seeds 1812 (W12) and World Seeds 1877 (W77). These varieties differ appreciably in economically valuable traits. The cultivars, F_1 and F_2 hybrids were raised in the field in 1972-1973, in two experimental variants differing in area of plant feeding: experiment 1 (exp-1), low-density sowing with 10×40 cm (400 cm^2) plant feeding area; experiment 2 (exp-2), usual density with 2×20 cm feeding area (40 cm^2). When scaled to 1 m^2 , the number of planted seeds constituted 25 in exp-1 and 250 in exp-2. We excluded from structural analysis plants that were raised with a marginal effect. We call attention to the fact that the number of kernels was determined as the average for all productive heads per plant, rather than for the main spike, as is erroneously done in many studies, since the yield of grain per unit area is determined by its weight in all spikes, rather than only the main ones. This approach enables us to obtain objective information about the nature of expression and inheritance of the most important element of the spike. Details of the experimental methods, description of base material and data about

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meteorological factors were given previously [2]. The tests for homogeneity of W_r-V_r revealed that the base material met all requirements imposed according to the hypothesis of Hayman [3], with respect to number of kernels per spike.

Experimental Section

The mean values of the trait for parents (\bar{x}) and hybrids from each recurrent parent (\bar{x}_0), which are listed in Table 1, indicate that there was considerable fluctuation of number of kernels per spike, depending on the genotype, vegetation conditions and plant feeding area. Under the conditions prevailing in 1972, there was formation of more kernels per spike than in 1973, and there were more in the case of low-density sowing (exp-1) than the usual density (exp-2). In 1972, the number of kernels ranged from 37.2 (W77) to 55.8 (P28) in exp 1 and from 24.9 (W77) to 44.1 (P28) in exp-2; in 1973, the figures were 28.8 (W77) to 48.4 (P28) and 19.6 (W12) to 33.3 (P28), respectively. With low-density sowing, an average of 6.6 more kernels were formed per spike in 1972 than in 1973, and with the usual sowing density, 7.7 kernels more in 1972.

Table 1. Number of kernels per spike in parents (\bar{x}) and hybrids (\bar{x}_0)

Cultivar	1972						1973					
	exp-1			exp-2			exp-1			exp-2		
	P	F ₁	F ₂	P	F ₁	F ₂	P	F ₁	F ₂	P	F ₁	F ₂
W12	43.2	43.8	42.3	29.4	32.1	31.2	36.5	34.1	19.6	24.2	23.2	
W77	37.2	42.8	40.4	24.9	30.2	28.8	35.7	32.4	20.5	24.3	21.6	
G ²⁹	40.8	41.7	41.8	30.1	32.0	33.8	35.7	34.3	23.3	25.2	24.9	
N7	39.1	42.9	42.7	29.2	31.8	35.2	36.7	34.7	24.2	24.8	25.1	
G ¹¹⁴	42.1	43.6	42.0	34.0	33.0	38.5	37.5	35.8	24.9	25.4	25.1	
P ⁵⁵³	38.5	42.1	41.6	31.2	32.3	34.5	35.0	34.5	22.6	24.2	24.3	
P ²⁸	55.8	51.0	49.5	44.1	37.0	48.4	41.8	41.4	33.3	28.9	28.7	
\bar{x}	42.4	44.0	42.9	31.8	32.6	35.8	37.0	35.3	24.1	25.3	25.1	
ncp with P<0.05		4.10			1.31		2.99			1.12		

As shown by the group means (\bar{X}), the hybrids as a whole formed more kernels per spike than the cultivars. We were impressed by the data obtained for P28, which is considerably superior to the others with regard to the trait in question, and this is indicative of the great genetic potential of this cultivar. Typically enough, the group means for hybrids (\bar{x}_0) were usually higher than the means (\bar{x}) for the recurrent parent. It is only in the combinations involving P28 that the means for the hybrids are significantly lower than the means for this cultivar. In most cases, the means are lower for F₂ hybrids than the means for F₁ hybrids.

The results of variance and covariance analysis listed in Table 2 indicate that, along with additive action, dominance also plays a substantial role in the system of genetic control of the character. The genetic components characterizing gene action and interaction differ in value, depending on vegetation conditions, plant feeding area and generation studied.

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There was the greatest stability found for component D, the values of which did not differ in 1972, and that of exp-1 in 1973 did not differ from 1972. Component \hat{F} was less stable. According to the results of evaluation of \hat{F} hybrids with low-density sowing in 1972, \hat{F} had a negative value, whereas in the case of usual sowing density that year and both experiments in 1973 it was positive; the value of \hat{F} was 2.7 times higher in 1973 with the larger feeding area (exp-1) than the usual area (exp-2).

Table 2. Results of variance and covariance analysis

Parameters	1972				1973			
	exp-1		exp-2		exp-1		exp-2	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
\hat{h}	35.36 ***	33.52 ***	35.61 ***	38.13 ***	30.70 ***	19.36 ***	10.16 ***	
\hat{p}	-15.30 ***	-10.79 ***	7.79 ***	8.10 **	-9.95 ***	2.97 ***	2.18 *	
\hat{h}_1	10.97 **	2.13	2.61 *	7.12 *	1.97	3.61 ***	3.28 **	
\hat{h}_2	10.75 **	1.98	2.50 *	9.36 ***	2.70	3.37 ***	2.98 **	
\hat{h}_0	5.69 *	1.36	1.38	2.48	1.16	4.39 ***	2.88 ***	
$(\hat{h}_1/\hat{h})^{1/2}$	0.56	—	0.27	0.44	—	0.43	0.41	
\hat{h}_1/\hat{h}_2	0.25	—	0.24	0.33	—	0.23	0.23	
$\frac{(4\hat{h}_1\hat{h}_2/\hat{h}) + \hat{p}}{(4\hat{h}_1\hat{h}_2/\hat{h}) - \hat{p}}$	0.44	—	2.34	1.66	—	1.43	1.22	
\hat{L}	3.75 *	5.59 ***	1.63	3.45 *	3.68 *	0.73 **	0.93 *	

Reliable with: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Note: The dashes indicate that indices were not calculated due to unreliability of one of the base parameters.

The value of parameter $(\hat{h}_1/\hat{D})^{1/2}$ was 2 times higher in exp-1 than exp-2, while no differences were demonstrable between experiments in 1973. The differences between components \hat{h}_1 and \hat{h}_2 were reliable only in exp-1 in 1973. The values of $\hat{h}_2/4\hat{h}_1$ in both 1972 experiments and in exp-2 in 1973 did not differ reliably from the 0.25 level. Parameter $(4\hat{h}_1)^{1/2} + (\hat{p}/(4\hat{h}_1))^{1/2}$ was greater than 1 in exp-2 in 1972 and in both experiments in 1973, but smaller than 1 in exp-1 in 1972. According to the results of evaluation of F_2 hybrids, parameters \hat{h}_1 and \hat{h}_2 were reliable in exp-2 in 1973; for this reason, indices characterizing the mean degree of dominance, proportion of genes with positive and negative effects, as well as proportion of dominant and recessive genes, were calculated only from the data of this experiment. These indices are similar to those obtained from the results for F_1 .

Table 3 lists the results of determination of parameter \hat{F}_r . As we see, the cultivars differed substantially in value of \hat{F}_r , which fluctuated as a function of vegetation conditions, plant feeding area and hybrid generation studied. According to the results for F_1 and F_2 , short-stemmed cultivars W12 and W77 were characterized by a negative value for \hat{F}_r in all cases. According to F_1 results, S29, M553 and P28 were characterized by a positive value for \hat{F}_r . For cultivars N67 and G114, negative values of

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\hat{F}_r were obtained from the results of evaluation of F_1 in exp-1 1972, whereas it was positive in exp-2 that year and both experiments in 1973.

Table 3. Values of parameter \hat{F}_r

Parent	1972				1973			
	exp-1		exp-2		exp-1		exp-2	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
W12	-75.85 ***	-41.84 ***	-14.27 ***	-23.15 ***	-47.68 ***	-16.81 ***	-27.15 ***	
S29	-45.70 ***	-12.18 **	-3.05 *	-24.35 ***	-23.40 ***	-10.11 ***	-3.17 *	
W77	27.85 ***	5.35 **	22.77 ***	19.70 ***	18.61 ***	4.41 ***	10.18 ***	
N67	-13.02 **	-3.46	18.74 ***	22.38 ***	7.84 ***	12.02 ***	12.44 ***	
G114	-19.81 **	-2.89	9.11 ***	19.78 ***	-11.78 ***	16.72 ***	5.07 ***	
M553	4.87	-29.84 ***	19.00 ***	24.17 ***	-11.64 ***	3.97 ***	8.41 ***	
P28	11.33 *	10.16 ***	3.21 *	19.72 ***	6.71 ***	12.97 ***	9.38 ***	

Reliable with: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The curves of regression of W_r as a function of V_r (Figures 1-4) yield a more complete idea about the system of genetic control of the character in each variety. According to data for F_1 hybrids in 1972, S29, P28 and M553 expressed significant dominance ($p \approx 50-75\%$) in the case of enlarged plant feeding area (see Figure 1a), whereas W77 and W12 presented recessiveness ($q \approx 75-100\%$). N67 and G114 were in the middle section of the line of regression, which is indicative of additive gene action, although parameter \hat{F}_r for these cultivars was reliable and indicative of some recessive gene expression. According to the results obtained for F_2 (see Figure 1b), in this experiment P28 and S29 expressed dominance ($p \approx 50-75\%$), while M553, W77 and W12 presented significant recessiveness ($q \approx 50-100\%$). There was expression of additive gene action in cultivars N67 and G114. This was confirmed by the fact that parameter \hat{F}_r was unreliable for these cultivars (see Table 3). According to the data obtained for F_1 in the case of usual sowing density in 1972 (see Figure 2), cultivars S29, N67, G114, M553 and P28 expressed different degrees of dominance ($p \approx 50-100\%$), while W12 and W77 expressed recessiveness ($q \approx 50-75\%$). In 1973, according to results for F_1 in the case of low-density sowing (see Figure 3a), P28, M553, S29, G114 and N67 expressed significant dominance ($p \approx 75\%$), and these cultivars differed insignificantly in nature of expression of dominance, as confirmed by the values of \hat{F}_r (see Table 3). W12 and W77 presented recessiveness ($q = 75\%$). According to results obtained on F_2 that year (see Figure 3b), the cultivars differed in nature of expression of dominant and recessive effects: S29, N67 and P28 manifested dominance ($p \approx 75\%$); W12, W77, G114 and M553 expressed different degrees of recessiveness ($q \approx 50-100\%$). According to data for F_1 in the case of low-density sowing (see Figure 4a), P28, G114, S29, N67 and M553 expressed dominance ($p \approx 50-75\%$), while W12 and W77 manifested recessiveness ($q \approx 75\%$). According to data for F_2 (see Figure 4b), there was no appreciable difference between cultivars in nature of expression of gene action, as compared to the results for F_1 .

As shown by the data submitted in Table 4, negative values were obtained in all experiments, according to the results of evaluation of F_1 and F_2 hybrids, for the coefficient of correlation between x and $W_r + V_r$; however,

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these values were unreliable in all cases, and this is related mainly to the small size of the sample ($n = 7$). The low coefficients of correlation (r) yielded low coefficients of determination (r^2), which were considerably smaller than 1. High and reliable coefficients of correlation were obtained between V_R and W_R ; moreover, the coefficients of regression of W_R as a function of V_R did not differ reliably from 1.

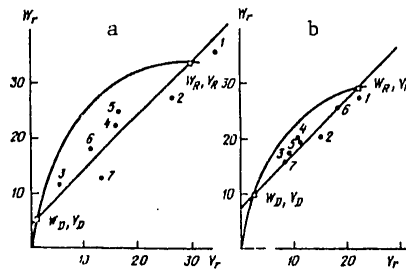


Figure 1.

Curves of regression of W_R as a function of V_R for F_1 (a) and F_2 (b), exp-1, 1972

- | | | |
|--------|---------|---------|
| 1) W12 | 4) N67 | 6) M553 |
| 2) W77 | 5) G114 | 7) P28 |
| 3) S29 | | |

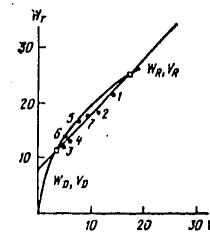


Figure 2.

Curve of regression of W_R as a function of V_R , F_1 , exp-2, 1972

Designations are the same as in Figure 1.

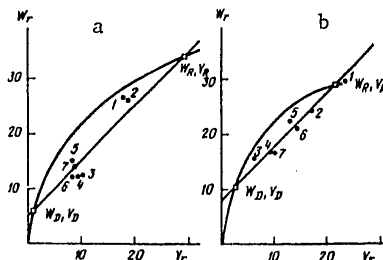


Figure 3.

Curves of regression of W_R as a function of V_R , for F_1 (a) and F_2 (b), exp-1, 1973

Designations are the same as in Figure 1.

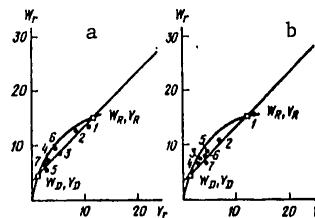


Figure 4.

Curves of regression of W_R as a function of V_R , for F_1 (a) and F_2 (b), exp-2, 1973

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Table 4. Results of correlation and regression analysis

Coefficients	1972				1973			
	exp-1		exp-2		exp-1		exp-2	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
r betw w_1 & v_1	-0.505	0.505	-0.025	-0.501	-0.494	-0.711	-0.548	
r' betw v_1 & w_1	0.351	0.161	0.081	0.319	0.244	0.505	0.300	
r_{w_1, v_1}	0.135 **	0.276 ***	0.067 ***	0.169 ***	0.187 ***	0.050 ***	0.504 ***	
r_{w_1, v_1}	1.053	1.160	1.018	0.110	1.049	1.130	1.190	

Reliable with: ** $P < 0.01$; *** $P < 0.001$.

Discussion

Analysis of the experimental data shows that the nature of expression and inheritance of the character under study changed significantly, depending on vegetation conditions (year) and plant feeding area (experiment). The cultivars used in the experiment differed substantially in degree of expression of the trait. Of the set of cultivars studied, late-ripening P28 stood out for its high genetic potential. We were impressed by the fact that the other late-ripening cultivar, M553, was considerably inferior to P28 in this respect. It must also be noted that diallele analysis of 10 wheat cultivars, made in Kazakhstan in 1973, demonstrated nonallelic gene interaction in P28, which was characterized by the largest number of kernels per spike under those conditions also [4, 5]. Among the average ripening cultivar group--S29, N67, G114--the last one was characterized by the highest genetic potential. Early ripening short-stemmed W12 and W77 were inferior to the others with regard to kernels per spike, although, as shown by the results of exp-1 in 1972, W12 was characterized by a rather high potential which, however, was not realized under the typical conditions of Siberia where poor water conditions are usually present at the early stages of plant development (June).

With regard to the system of genetic control of the trait as a whole, it should be noted that, along with genes expressing additive action, a significant contribution is also made by genes with dominant action to the number of kernels per spike. We were impressed by the fact that the dominant effect for kernels per spike is expressed more than for such spike traits as number of spikelets per spike and spike length [2, 6].

It is remarkable that significant stability was demonstrable in component \hat{D} , which characterizes additive gene action, according to number of kernels. Under the conditions of 1972, the values of \hat{D} did not differ in different experiments, whereas in 1973 they were close to the levels obtained in 1972 with low-density sowing. It is only with limited plant feeding area (exp-2) in 1973 that the value of \hat{D} was almost one-half that obtained with the larger feeding area (exp-1). Consequently, in the case of the larger plant feeding area, not only was there fuller realization of the genetic

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potential of the cultivar, but more stable expression under different vegetation conditions of the part of the genetic information determined by genes with additive action. Of course, this cannot be said of the genetic parameters characterizing allelic gene interaction. In the case of low-density sowing in 1972, component F , which reflects the direction of dominance on the whole for the material tested, was characterized by a negative value, whereas in the other experiments it was positive. The change in direction of dominance is indicative of complex interaction between allelic genes and between the genotype as a whole and environmental conditions in the process of ontogenesis. The negative value of F is related primarily to the distinctions of the system of genetic control of the trait in the early-ripening, short-stemmed cultivars W12 and W77. It should be noted that, unlike the other spike characters we studied previously [2, 6], similar values of F for number of kernels were obtained in evaluation of F_1 and F_2 hybrids.

The results obtained in 1972, when parameter $(\hat{H}_1/\hat{D})^{1/2}$ which reflects the mean degree of dominance as a whole for the material studied, was twice the value in the case of enlarged feeding area, as compared to the usual area, were indicative of considerable interaction between dominant genes and the environment, whereas in 1973 this parameter was similar in the different experiments. While a disproportion of alleles with positive and negative effects, according to action on development of the trait, was observed in most cases for spike length [6], it is only in the case of low-density sowing in 1973 that the value of parameter $\hat{H}_2/4\hat{H}_1$ deviated reliably from the 0.25 level. This indicates that there was some excess of alleles with positive effects in the experiment with enlarged plant feeding area in 1973. It was also typical that an excess of genes with recessive action was observed in 1972 only in the case of low-density sowing, whereas in all other experiments there was a significant excess of genes with dominant action. Parameter \hat{F}_R , which reflects the relative contribution of additive and allelic gene interaction, was relatively stable as a function of vegetation and experimental conditions for number of kernels per spike, unlike other traits studied [2, 6, 7]. Suffice it to indicate that only positive values of \hat{F}_R were obtained for cultivars S29, M553 and P28 as a result of evaluation of F_1 , and only negative ones for W12 and W77. This is indicative of a certain stability of direction of dominance in these cultivars. A change in direction of dominance was observed in N67 and G114, depending on vegetation conditions, in the case of low-density sowing.

The curves of regression of W_R as a function of V_R are an excellent illustration of variability of relative contribution of dominant and recessive alleles to phenotypic development of the trait, depending on vegetation conditions, density of plant stands and hybrid generation studied. Although the order of the cultivars on lines of regression according to number of kernels per spike changed in different years, experiments and generations studied, this change was not as marked as for stem length [7], spike length [6] and number of spikelets per spike [2].

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It is imperative to determine the nature of gene influence on development of the character during ontogenesis in order to perform tasks related to refinement of this trait by means of selection. As shown by correlation analysis, negative values were obtained in all experiments for the coefficient of correlation between mean values of the trait in parents and level of dominance. Although these coefficients are unreliable, because of the small size of the sample, they reflect rather clearly the effects of genes on development of the character. In only one case (exp-2, 1972) the coefficient of correlation was very low. Dominant genes induce positive effects on phenotypic expression of the trait and recessive ones induce negative ones. In all of the experiments, the correlation between x and $W_r + V_r$ was negative, which makes it easier to predict the effectiveness of breeding for improvement of the character on the basis of the tested assortment of cultivars. However, as shown by the forecast, the expected maximum refinement of the trait reaches the level inherent in P28, which was considerably superior to other cultivars in number of kernels per spike in all of the tests.

Thus, we see that P28 is a unique source of genes that must be used intensively in breeding programs. If we add to this that all of the locally raised and promising cultivars that are being tested and grown in the Siberian region are substantially inferior to that cultivar in number of kernels per spike, it becomes understandable that P28 is of great value in solving breeding problems directed toward increasing the productivity of soft wheat spikes. In view of the fact that this cultivar forms a relatively small kernel, as compared to the best Siberian cultivars, we can conclude that there are considerable possibilities for increasing spike productivity by means of recombination of genes controlling kernel size and number of kernels per spike. If recombinants are obtained as a result of transgressive segregation, in which the number of kernels per spike will remain at the level of P28, but grain weight will increase, we can expect considerable increase in spike productivity. Of course, such recombinants can be obtained only in the absence of close linkage between genes that control these traits.

In view of the fact that the number of kernels per spike is controlled by an additive-dominant genetic system, which was expressed particularly well and with relative stability in different years and experiments in cultivars P28, S29 and M553, it is feasible to perform selection in early segregating generations (F_2 - F_3). It is remarkable that dominant genes induced positive effects on phenotypic expression of the character; therefore, rather effective selection is expected, even though the recombinants selected in the early segregating generations may segregate genotypes with fewer kernels per spike in later generations. To enhance the effectiveness of selection in segregating hybrid generations, the material must be grown with low-density sowing and uniform plant feeding area. Since the trait is controlled by a large number of genes, each of which contributes a negligible effect on phenotypic expression of the character, one should raise a rather large number of F_2 or F_3 plants for

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selection. It is quite apparent, that the quantity thereof depends on the hybrid combination. Very many plants will have to be grown of hybrids involving short-stemmed cultivars W12 and W77 in order to obtain the desired recombinant as a result of transgressive segregation. The quantity can be reduced significantly if dealing with G114×P28, N67×P28, S29×P28 and M553×P28 hybrids, in which the effectiveness of selection will be rather high in an F₂ population consisting of 3000-5000 plants.

With reference to trait improvement through selection, it must be borne in mind that we have been dealing here only with number of kernels per spike. In actual practice, much more complex tasks are involved in any breeding program. Not infrequently, these tasks are unrealistic, in the sense that one cannot expect a positive solution to a given problem on the basis of the initial material used in the crosses. As a rule, breeding programs have the goal of improving an entire set of traits, each of which is controlled by a specific genetic system. Without knowledge about these systems, it is impossible to develop effective breeding programs and to implement them according to plan. In this respect, diallele analysis is unquestionably the most effective means of learning about the system of genetic control of a quantitative character and about the interaction of this system with environmental conditions.

BIBLIOGRAPHY

1. Tsil'ke, R. A. "Study of Inheritance of Quantitative Characters in Soft Spring Wheat Topcrosses. Report 5: Number of Kernels Per Spike," GENETIKA [Genetics], Vol 13, No 11, 1977, 1889.
2. Tsil'ke, R. A.; Kachur, O. T.; and Sadykova, S. A. "Variability of Genetic Parameters in Diallele Analysis of Quantitative Characters of Soft Spring Wheat. Report 1: Number of Spikelets per Spike," Ibid, Vol 14, No 8, 1978, 1409.
3. Hayman, B. I. "The Theory and Analysis of Diallele Crosses," GENETICS, Vol 39, 1954, 789.
4. Kalashnik, N. A., and Molin, V. I. "Evaluation of Spring Wheat Cultivars for Breeding Purposes According to Their Hybrids," GENETIKA, Vol 11, No 1, 1975, 5.
5. Idem, "Genetic Control of Quantitative Characters in Spring Wheat," Ibid, Vol 10, No 11, 1974, 17.
6. Tsil'ke, R. A.; Kachur, O. T.; and Sadykova, S. A. "Variability of Genetic Parameters in Diallele Analysis of Quantitative Characters of Soft Spring Wheat. Report 3: Spike Length, Ibid, Vol 15, No 2, 1979, 286.

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7. Tsil'ke, R. A.; Kachur, O. T.; and Sadykova, S. A. "Variability of Genetic Parameters in Diallele Analysis of Quantitative Characters of Soft Spring Wheat. Report 2: Stem Length," GENETIKA, Vol 15, No 2, 1979, 273.
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